Planktonic interactions and particulate flux in Ellis Fjord, east Antarctica

by

Karin Louise Beaumont B. App. Sc., Grad. Dip. (Hons)

Submitted in fulfilment of the requirements
for the degree of Doctor of Philosophy

University of Tasmania
Hobart

February 2003

Declaration

This is to certify that the material contained in this thesis has never been accepted for any other degree or award in any tertiary institution and, to the best of my knowledge and belief, is solely the work of the author, and contains no material previously published or written by another person, except where due reference is made in the text.

Karin L. Beaumont

23 June 2003

Authority of Access

This thesis may made available for loan and limited copying in accordance with the Copyright Act 1968.

Karin L. Beaumont

23 June 2003

Abstract

The Southern Ocean is one of the largest marine ecosystems in the world, and is a major sink for atmospheric carbon dioxide. Thus, it plays a considerable role in the mitigation of the greenhouse effect and resultant global warming. Marine micro-organisms dominate the plankton biomass in Antarctic waters, consume much of the primary production, and are principal determinants of the transfer and vertical flux of photosynthetically-fixed carbon. This thesis examines the composition and trophodynamics of a plankton community dominated by microzooplankton grazers, and their role in vertical carbon flux in an east Antarctic fjord. Ellis Fjord is a semi-isolated marine inlet that is usually ice-covered throughout the year, and supports a zooplankton community that has low species richness and is dominated by microzooplankton. As such, it is akin to a macrocosm in which the role of microzooplankton in carbon dynamics can be studied in detail, in the relative absence of strong hydrodynamic forcing and the influence of higher trophic levels.

The seasonal succession of the plankton community in Ellis Fjord was similar to that commonly observed in the wider Southern Ocean; changing from dominance by microplanktonic diatoms and small herbivorous copepods during early summer to nanoflagellates and protozoa during late summer. Microplanktonic diatom blooms and herbivorous grazers are commonly regarded as contributing to carbon export in the Southern Ocean, while communities dominated by auto- and heterotrophic nanoplankton favour the retention and respiration of carbon in pelagic waters. In Ellis Fjord, the physiological state of the cells appeared to determine their buoyancy, as microplanktonic diatoms did not directly sediment until the bloom declined. While there was evidence of near-surface export of microplanktonic diatoms, heterotrophic nanoflagellates, and microzooplankton faecal pellets, these contributed little to vertical flux to depth. Grazing by microzooplankton retarded the flux of phytoplankton by reducing the number of cells available to sediment directly, by producing faecal pellets of a morphology and ultrastructure that inhibited sinking, and by coprophagous degradation and recycling of pellets.

Most pellets at depth were minipellets that contained little carbon, many of which appeared to be 'false' minipellets caused by coprophagy and degradation. Surprisingly, protozoan pellets that contained only empty diatom frustules contained more carbon per pellet than small oval copepod pellets. Differences in the ecology of the dominant small copepods, *Oithona similis* and *Oncaea curvata*, affected the morphology, persistence, and carbon content of their pellets, and the distribution of their biomass in the water column. Despite differences within and between small copepod and protozoan taxa, models of carbon flux in Ellis Fjord indicate that these microzooplankton contribute to the retention of both new and regenerated production. This reduces the draw-down of atmospheric carbon in Antarctic waters and the capacity of these waters to ameliorate global climate change.

Acknowledgements

Thanks go to my supervisors...

To Assoc Prof David Ritz particularly for handling all the administrative side of things;

To Dr Graham Hosie for introducing me to the world of microscopic plankton, for giving me the opportunity to fulfill a childhood dream to visit Antarctica, employing me at regular intervals, and for generally being so supportive, understanding, and happy to have a chat over a beer or two;

To Dr Kerrie Swadling for her friendship, for first suggesting I work in Ellis Fjord that allowed me to experience the beauty of the Antarctic continent, for all her help and personal support, while she was finishing her own PhD, prior to officially becoming a supervisor on this project, as well as for all the subsequent assistance and just 'being there' whenever she could.

Thanks are also extended to...

Drs Andrew Davidson & John Gibson for always willing to give up their time to read drafts, provide valuable comments, and offer advice and encouragement.

Dr Steve Nicol for stepping in to read drafts when my supervisors were absent, providing employment, being good natured, and for his attempts to be humorous (!). Most importantly, for providing me with a laptop computer for the write-up of this thesis. In answer to your repeated question... have you finished yet? The answer is YES!

Prof Harvey Marchant for his encouragement and useful discussion particularly at the beginning of my PhD, for reading drafts, use of his library, and for approving and accommodating my need for employment.

To the following people overseas who provided useful discussion and/or provision of unpublished data: Prof Victor Smetacek, Dr Jeff Turner, Dr Juanita Urban-Rich & Dr Anna Pasternak. I also acknowledge the provision of unpublished data from Drs Kerrie Swadling, John Kirkwood & John Bowman.

To Dr Juanita Urban-Rich for putting me in touch with Horn Point Laboratory. To Lois Lane of Horn Point Laboratory, University of Maryland Systems, Maryland, USA, for running the faecal pellet carbon samples. Graham Rowbottom of the Central Science Laboratories, University of Tasmania, for running the POC samples, and for enjoying the mud cakes!

For assistance in Antarctica...

To Anthony Plummer for being a great fieldy, and particularly for putting up with me when I was so stressed out.

To all the Davis crew for field assistance, and general support. To the various station leaders, particularly Dr Joe Johnson for cheerfully accommodating my logistic requirements. Also to Clobbs, Psycho, Snarby, Mayhem, Gadgets & the Gimp who were happy to brave the often awful weather to assist me in drilling copious numbers of holes through thick sea-ice, and to drive rubber boats in wet, windy conditions, and the particularly memorable time of ice-breaking while in the rubber duckys! Also special mention to the chopper crew: Steve of 'Whisky Charlie India' for getting up early on Sunday mornings to ferry me to my sampling site, and to Rob McPhail and the team for all their attempts to get us off the continent, for sticking to their decisions to ensure our safety, and eventually getting us to the ship.

For technical assistance at the Australian Antarctic Division (AAD)...

To Debbie Lang & Trevor Bailey for the provision of laboratory work-space and consumables, and assistance with laboratory equipment.

To John Kitchener, Rick van den Enden, & Gerry Nash, for all their technical assistance particularly with all those little bits and pieces that are so important, as well as for their good humour and understanding that helped keep me sane! In particular to John for all his help during the final stages!

To Kevin Bell, Rene Wanless, Wayne Papps, & Glenn Jacobson from the Multimedia Unit, for assistance with Figures 4.3-4.5, as well as providing me with a period of employment, and for generally being bright, cheerful and always willing to help.

To John Cox of Science Technical Support for drafting Figures 1.1, 2.1 and Appendix 1, and for cheerfully assisting with subsequent formatting.

To Ben Raymond of the Antarctic Data Centre, AAD for assisting with Statistica problems, and putting me in touch with Richard Fraccaro of Statsoft. To Richard whose assistance and instruction with Statistica over the phone was truly wonderful! and to Steven Candy, AAD for cheerfully giving his time, at short notice, to provide me with advice and assistance with statistics.

On a more personal note, to Judith Wolters of Executive AAD, Cheryl & Anne of General & Window Cleaning, and the guys from Chubb security, for passing a smile and a chat that helped to break the long hours...

Official thanks...

To the AAD for tremendous support by numerous personnel, and provision of work-space, laboratory and other facilities, as well as the many wonderful employees who made it such a pleasant working environment.

The work in this thesis was supported by two Antarctic Science Advisory grants (963 & 2227). I also acknowledge the Queen's Trust that provided a grant to enable my attendance and presentation of part of this thesis at the 7th International Conference on Copepoda, Curitiba, Brazil, 25-31 July 1999.

Friends & family...

To all my special friends dotted around the globe – thanks for your supportive emails, and for being patient with me, when my promises to visit once I finished the PhD echoed over more years than they should have!

To my friends here, particularly Lou & Kelvin, for putting up with my pre-occupation over a number of years... forgiving my neglect..., and still inviting me to dinner!

To Steph & Mandy for their friendship and understanding, and for dropping in the occasional meal in those last few weeks of chaos!

To those people I have probably neglected to mention, it is not through lack of appreciation, but through sheer exhaustion!

Finally, to my Mum for all the phone calls and 'care' packages;

To James and Erica, for accepting me into family life and then abiding my absences from it;

and to Clobbs... well, you know what for... for your continual assistance, advice, and input to this thesis, and your constant support, love, understanding, and belief in me, as well as much more that I cannot express in words... Love you! and here's to a new beginning...

Table of Contents

Introduction

To predict the effect of global climate change on the structure and function of the world's ecosystems requires the investigation of the processes that regulate global climate. Increased levels of greenhouse gases in the atmosphere and resultant global warming have led scientific research to focus on oceanic carbon flux, particularly at the polar regions as they appear most susceptible to climate change. The oceans have the potential to mitigate increased concentrations of CO_2 in the atmosphere as a result of the photosynthetic uptake of carbon by phytoplankton (e.g. Longhurst 1991, Siegenthaler & Sarmiento 1993, Denman et al. 1996). The capacity of the oceans to act as a carbon sink is dependent upon the magnitude and fate of phytoplankton biomass that is, in turn, determined by the physical environment, and the structure and trophodynamics of the plankton community (e.g. Arrigo et al. 1999, Falkowski et al. 2000, Marchant et al. 2001).

Most studies investigating oceanic carbon flux have focused on quantitative measurements of the chemical composition of material collected by sediment traps moored in the oceans (e.g. Matsuda et al. 1987, Matsuda et al. 1990, Nelson et al. 1996, Cripps & Clarke 1998). While such quantitative estimates contribute to our knowledge of the magnitude of carbon flux, they do not contribute to an understanding of what regulates vertical flux in marine systems (Wassmann 1998). Zooplankton (heterotrophic protozoan and metazoan) grazing plays a crucial role in oceanic carbon transfer and flux (Michaels & Silver 1988, Marchant & Murphy 1994, Banse 1995a, Le Fèvre et al. 1998). Zooplankton repackage phytoplankton cells into compact faecal pellets that contribute to downward flux, and contribute to the transfer of carbon between trophic levels in the pelagic zone via ecological interactions such as competition and predation (Hairston & Hairston 1993). These interactions are dependent on individual species' life-history strategies, morphologies, and behaviour (Fenchel 1988, Boero 1994, Verity & Smetacek 1996). However, attempts to investigate carbon flux through planktonic systems using food web models have generally ignored species-specific interactions, and included only broad taxonomic groups (e.g. Michaels &

Silver 1988, Rivkin et al. 1996). Consequently, such models do not account for individual species' ecologies and tend to "simulate trophic functions dispersed among taxa, rather than the purported function-specific taxonomic units" (Longhurst 1991).

The role of individual species' ecologies and interactions in regulating vertical flux has been touched upon in biogeochemical studies of northern waters (reviewed in Wassmann 1998). However, the high biodiversity of species in the ocean, together with logistical constraints, has resulted in a lack of detailed taxonomic studies of plankton trophodynamics across a range of habitats. An east Antarctic fjord, Ellis Fjord, provides an ideal location for fine-scale studies of planktonic interactions and biogeochemical processes (Trull et al. 2001). While the fjord supports a range of planktonic organisms that are representative of those in the wider Southern Ocean, species diversity is low (Kirkwood 1993), and the semi-enclosed nature of the fjord results in a relatively discrete zooplankton community that is generally isolated from the influence of higher trophic levels and strong hydrodynamic forcing. Furthermore, the proximity of the fjord to Australia's Davis station permits fine-scale temporal observations over long periods.

This thesis examines the role of planktonic interactions in regulating vertical carbon flux. The first chapter describes the physical characteristics of the study site, and summarises the current knowledge of plankton dynamics and sedimentation in Ellis Fjord. Chapter 2 reviews the design of sediment traps and the use of poisons and preservatives, and justifies the sediment trap design and choice of poison used in this study. The plankton community composition is presented in Chapter 3, and the species interactions, seasonal succession, and trophodynamics discussed in relation to their life-history strategies. Results show that microzooplankton dominate the grazer community in the fjord, and a detailed investigation of the ultrastructure, morphology and flux of their faecal pellets forms Chapter 4, while Chapter 5 examines the size-fractionated flux of the phytoplankton community through the water column. The role of direct sedimentation of phytoplankton versus grazer-mediated flux is subsequently examined via models of carbon fluxes that are developed using taxa- and species-specific data from previous chapters (Chapter 6). Finally, conclusions are drawn from this research examining the role of these micro-organisms in carbon flux in Antarctic

coastal waters, and how changes in planktonic community structure due to global warming could affect the capacity of Antarctic waters to ameliorate global climate change.

Chapter 1

Description of Ellis Fjord

Ellis Fjord is a semi-enclosed inlet that has marine characteristics for most of the year, with the exception of a freshwater melt lens that occurs during summer (Kirkwood 1993). It is therefore distinct from other fjords that exhibit a gradient from freshwater to the sea, and is akin to other Antarctic marine waters in that it supports a biological community similar to that reported in the wider Southern Ocean (Boden 1985, Syvitski et al. 1987, Kirkwood 1993, Smith & Tréguer 1994, Kopczynska et al. 1995). The semi-enclosed nature of the fjord and its proximity to Australia's Antarctic research base, Davis station, provides the opportunity to study intra- and inter-seasonal changes in community dynamics at fine temporal scales, which is often logistically difficult in the open ocean. This chapter reviews the existing knowledge of the biological community composition and biogeochemistry of Ellis Fjord. While the entire fjord is described, it should be noted that the research in this thesis was undertaken only in Middle Basin.

1.1 Hydrography

Ellis Fjord, which is located in the Vestfold Hills, Antarctica (68°35'S, 78°00'E, Figure 1.1a), is approximately 10 km long and 1 km wide. However, the entrance to the fjord is only 160 m wide and has a sill that is <3 m deep (Kirkwood 1993, Figure 1.1b). It lies along a geological weakness zone and was presumably formed by selective glacial-scouring of the narrow bands of metamorphic rocks (Adamson & Pickard 1986a), and subsequent isostatic uplift of the land relative to the sea (Adamson & Pickard 1986b). The fjord contains five major basins, ranging in depth from 13 m to 117 m, that are separated by a series of sills (Gallagher & Burton 1988, Figure 1.1b). From mid-January to February, in most summers, freshwater from the ice plateau and the Sørsdal glacier flows through Ellis Rapids into the fjord (Gallagher & Burton 1988, Kirkwood 1993). This freshwater input, coupled with limited mixing with the open ocean due to the narrow fjord entrance from the sea

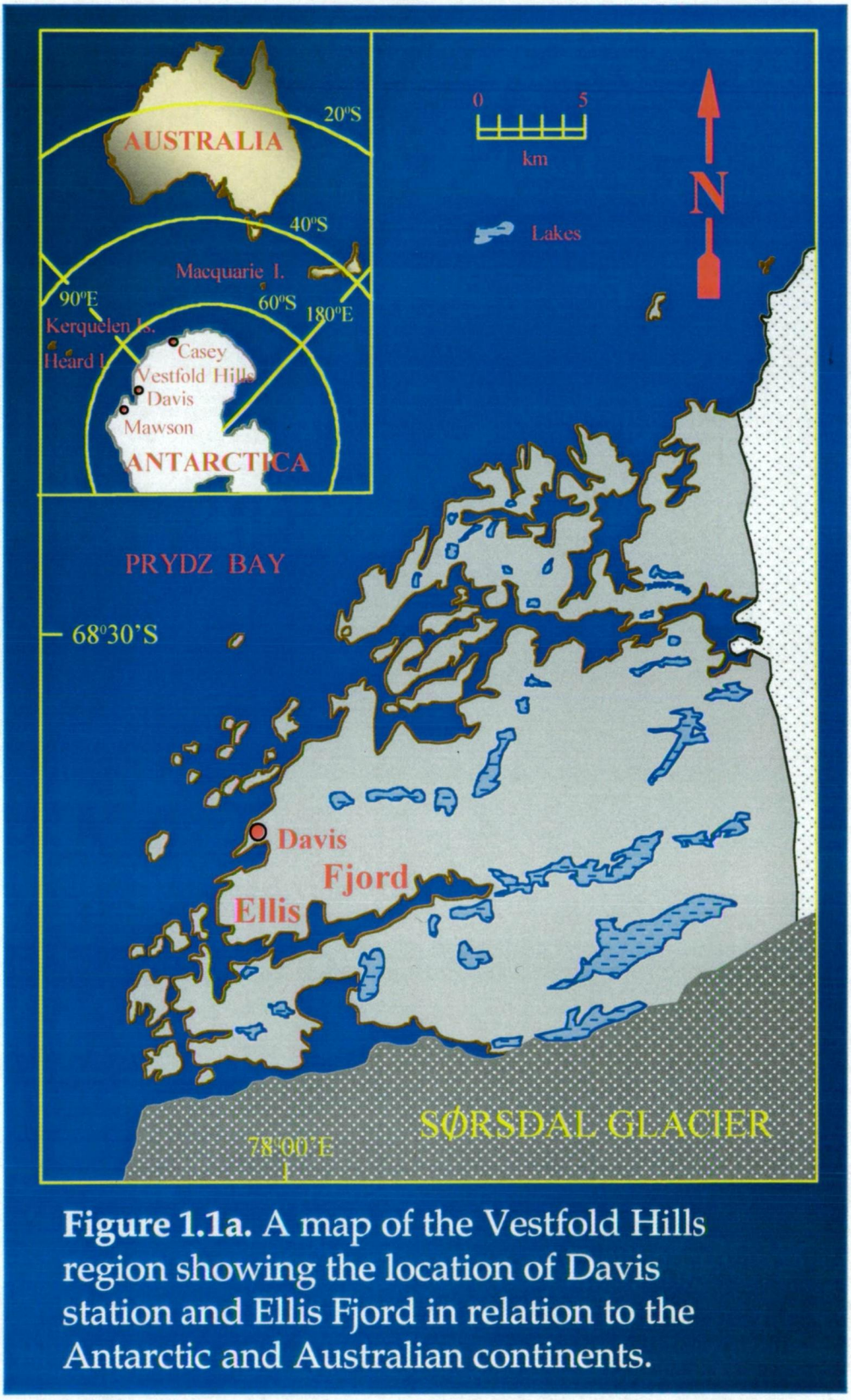


Figure 1.1a. A map of the Vestfold Hills region showing the location of Davis station and Ellis Fjord in relation to the Antarctic and Australian continents.

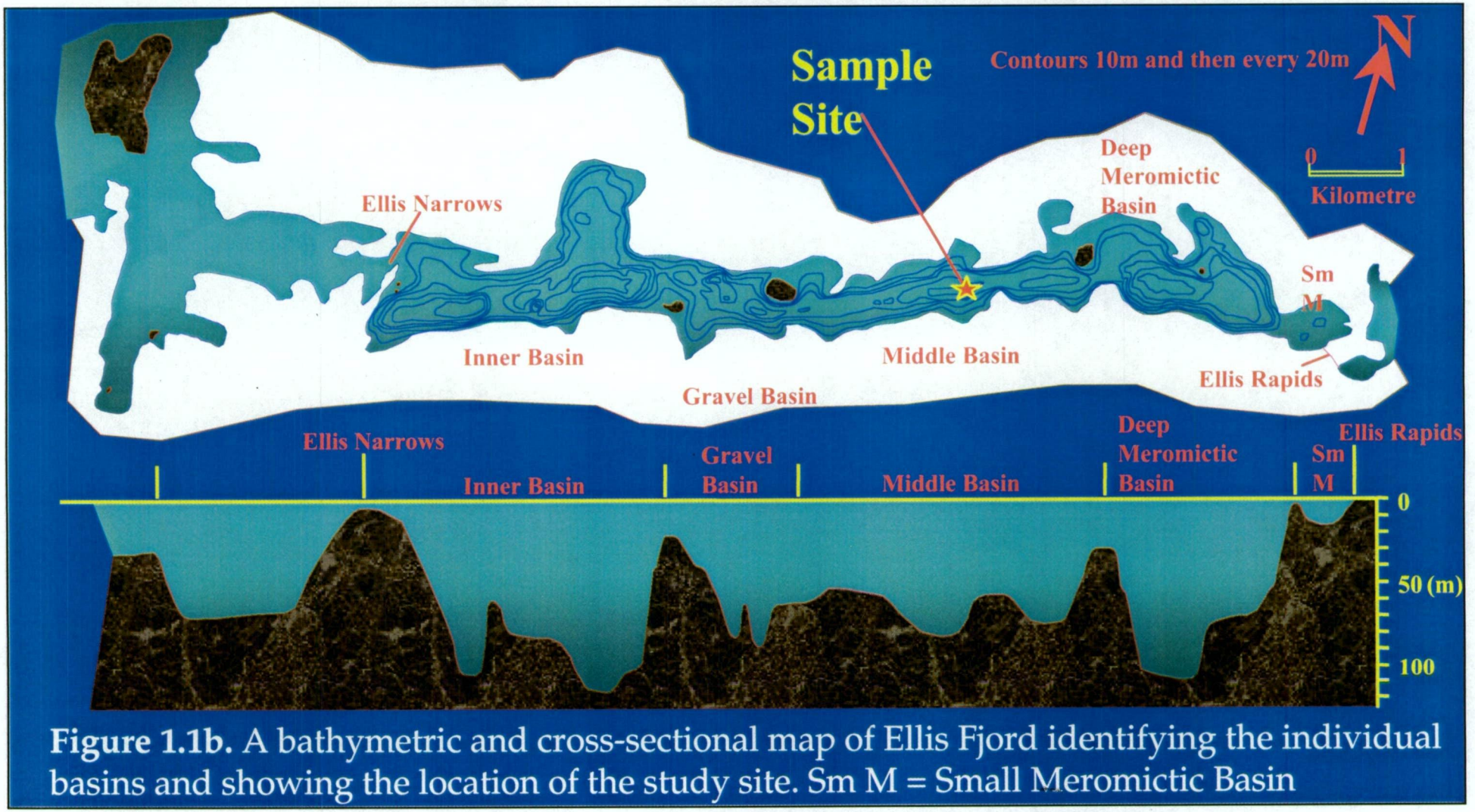


Figure 1.1b. A bathymetric and cross-sectional map of Ellis Fjord identifying the individual basins and showing the location of the study site. Sm M = Small Meromictic Basin

(Ellis Narrows; Figure 1.1b) and decreased tidal influence along the fjord, leads to vertical stratification in the two landward basins (Kirkwood 1993). In summer, these basins comprise a freshwater surface layer, a middle oxic seawater layer, and a deeper hypersaline, sulphide, anoxic water layer (Burke & Burton 1988, Gallagher et al. 1989).

Ellis Fjord is covered by 1-2 m of ice for most of the year (Kirkwood 1993, Gibson 1998). However, the mouth of the fjord, Ellis Narrows, is usually ice-free during summer due to the shallow sill and strong tidal flow (Gallagher & Burton 1988, Kirkwood 1993). There has been considerable interannual variation reported in the extent of ice-cover over the entire fjord during summer (Table 1.1). Such interannual variation in ice formation affects the mixing intensity in the fjord, with ice-free summers leading to intensive mixing of the water column, while the maintenance of ice-cover throughout summer leads to reduced mixing and stratification (Gibson 1999). This variability in mixing influences nutrient concentrations in the water column, and this is reflected in the biological community composition and biogeochemistry of the fjord.

Despite the long periods of daylight during the Antarctic summer, the maintenance of at least partial ice-cover during most years leads to low light levels in the underlying water column; only 0.2–10% of the incident light is transmitted, resulting in irradiances between 3 and 18 $\mu E\ m^{-2}\ s^{-1}$ (Kirkwood 1993, Gibson 1998). The water temperature ranges from –1.9°C during winter, to 0°C in near-surface waters during summer. Salinity is around 34 for most of the year but decreases during summer to below 33 due to the freshwater lens that results from the melting ice-cover and / or the transport of low salinity water from other basins (Kirkwood 1993, Gibson 1998).

Table 1.1. Summary of observations of the extent of ice-cover during summer (December - February) at Ellis Fjord. Where only a single year is given e.g. 1981, the exact summer i.e. 1980/1 or 1981/2 was not specified. F = Full ice-cover, P = Partial ice-melt, I = Ice-free

	F	P	I	Reference
1946/7			*	Gallagher & Burton (1988)
1974/5			*	Gallagher & Burton (1988)
1981			*	McMinn (1994)
1982		*		McMinn (1994)
1983		*		McMinn (1994)
1984		*		McMinn (1994)
1985/6	*			Gallagher & Burton (1988)
1986		*		McMinn (1994)
1987	*			McMinn (1994)
1988			*	McMinn (1994)
1989		*		McMinn (1994)
1990		*		McMinn (1994)
1991			*	McMinn (1994)
1992/3	*			McMinn et al. (1995)
1994/5	*			Gibson (1998)
1995/6		*	*	French pers comm.
1996/7		*		Thomson pers comm.
1997/8		*		this study
1998/9			*	Heil pers comm.
1999/00	*			Heron pers comm.

1.2 Planktonic community

1.2.1 Microbes

Both the fast-ice and the water column in Ellis Fjord support a diverse bacterial community that is generally typical of that reported in the Southern Ocean (Table 1.2, Bowman et al. 1997a,b). The exception is the

Table 1.2. Bacterial taxa identified from the sea-ice and water in Ellis Fjord (J.P. Bowman, pers comm.).

Sea-ice	Sea-water
Flavobacteria	
Cellulophaga algicola	*Polaribacter* spp.
Cellulophaga spp.	
Gelidibacter algens	
Gelidibacter spp.	
Psychroserpens spp.	
Brumimicrobium glaciale	
Polaribacter irgensii	
Polaribacter franzmannii	
Polaribacter spp.	
Psychrobacter glacincola	
Flavobacteriaceae	
several novel *Cytophaga*-like strains	
Alpha proteobacteria	
Octadecabacter spp.	*Sphingomonas* spp.
	Hyphomonas johnsonii
	Hyphomonas spp.
Gamma proteobacteria	
Shewanella figidimarina	*Halomonas variabilis*
Glaciecola punicea	*Shewanella frigidimarina*
Glaciecola pallidula	*Psychrobacter immobilis*
Glaciecola spp.	*Psychrobacter glacincola*
Pseudoalteromonas antarctica	*Psychrobacter* spp.
Pseudoalteromonas prydzensis	*Pseudoalteromonas antarctica*
Marinobacter spp.	*Pseudomonas* spp.
Pseudomonas spp.	
Psychromonas spp.	
Firmicutes	
Planomicrobium mcmeekinii	
Planococcus spp.	
Actinobacteria	
Arthrobacter spp.	*Arthrobacter agilis*
	Micrococcus luteus
	Janibacter spp.

presence of the photosynthetic sulphur bacteria *Chlorobium* spp. that occur at the O_2 - H_2S interface in the upper meromictic basins (Burke & Burton 1988). In the oxic basins, that comprise the majority of the fjord, the annual cycle of bacterial abundance appears to follow the concentration of chlorophyll *a*, increasing during late spring to a maximum in summer (Grey et al. 1997). Unidentified heterotrophic nanoflagellates are also present in the fjord and show a similar seasonal pattern of abundance (Grey et al. 1997).

1.2.2 Phytoplankton

The phytoplankton community in Ellis Fjord is mostly composed of diatom, nanoflagellate, and dinoflagellate taxa (Table 1.3), with their relative dominance in the community changing throughout the year. Diatoms dominate the fast-ice algal assemblage during spring and are released into the water column during ice-melt. This results in an increase in phytoplankton abundance in upper waters prior to the rapid sedimentation of these cells to depth. Consequently, the ice-algal bloom makes little contribution to *in situ* planktonic growth (McMinn 1996). Rather, the summer phytoplankton bloom is composed of planktonic species that have encysted in the fjord, or have been advected with water masses along the fjord. These phytoplankton species are photo-adapted to low light levels (<18 $\mu E\ m^{-2}\ s^{-1}$, see above), resulting in the development of substantial phytoplankton blooms under the ice (Gibson 1998). These blooms are alternately dominated by diatoms and flagellates, a phenomenon that appears driven by the limitation of available silica in the water column and/or the extent of ice-melt and mixing in the fjord (McMinn et al. 1995, Gibson 1999).

By late summer dinoflagellate concentrations increase and this taxon dominates the phytoplankton community during winter, albeit in low concentration: the combined concentration of auto- and heterotrophic species ranges from 1×10^2 to 5×10^4 cells L^{-1} (Grey et al. 1997, Gibson 1998). It is likely that some species inhabit and encyst in the fast-ice during winter as their cysts are generally common in ice-algal assemblages, and

Table 1.3. The dominant phytoplankton taxa in Ellis Fjord. Note, the study by McMinn & Hodgson (1993) was only during summer, while the other two studies encompassed a winter and summer period. IB = Inner Basin, MB = Middle Basin.

IB 1991/2 McMinn & Hodgson (1993)	MB 1994/5 Gibson (1998)	MB 1992/3 Grey et al. (1997)
Diatoms		
Chaetoceros spp.	*Fragilariopsis curta*	Not investigated
Nitzschia cylindrus	*Thalassiosira australis*	
Thalassiosira australis	*Thalassiosira dichotomica*	
Thalassiosira dichotomica	*Thalassiosira antarctica*	
Entomoneis kjellmanii	*Entomoneis kjellmanii*	
Berkeleya rutilans	*Berkeleya rutilans*	
Navicula glacei	*Porosira socialis*	
Flagellates		
Cryptomonas sp.	*Cryptomonas* sp.	Not specified
Pyramimonas geldicola	*Pyramimonas geldicola*	
Phaeocystis antarctica	*Phaeocystis* c.f. *antarctica*	
Dictyocha speculum		
Dinoflagellates		
Not specified	*Gymnodinium* spp.	*Gonyaulax* sp.
	Ampidinium spp.	*Gymnodinium* sp. 1
	Gymnodimnoid cyst	*Gymnodinium* sp. 2
		Gymnodinium sp. 3

the abundant Antarctic fast-ice species *Polarella glacialis* has been recently identified from the ice in Ellis Fjord (Thomson 2000).

1.2.3 Protozoa

Ellis Fjord supports a diverse range of ciliate species and heterotrophic dinoflagellates (Table 1.4). However, investigations of the succession of protozoan species have not been as extensive as that of the phytoplankton species in the fjord. Their pattern of abundance appears to follow that of autotrophic dinoflagellates described above, increasing during late summer, and maintaining a presence throughout winter (Grey et al. 1997, Gibson 1998). Similar to dinoflagellates (see above), ciliate concentrations have been reported to be low reaching a maximum of 2.2×10^3 cells L^{-1} in summer, and <20 cells L^{-1} during winter (Grey et al. 1997).

Table 1.4. The dominant dinoflagellate and ciliate taxa in Middle Basin, Ellis Fjord recorded from January to November 1993 (Grey et al. 1997).

Dinoflagellates	Ciliates
Dinophysis contracta	*Lohmanniella oviformis*
Gyrodinium rhabdomante	*Strobilidium* sp. 1
Peridinium sp. *cf umbonatum*	*Strobilidium* sp. 2
Protoperidinium metanum	*Strombidium* sp. 1
Protoperidinium defectum	*Strombidium acutum*
Protoperidinium mediocre	*Tontonia* sp. 1
Protoperidinium charcoti	*Tontonia* sp. 2
Protoperidinium sp.	*Codonellopsis gaussi*
	Laackmanniella naviculaefera
	Cymatocylis drygalskii
	Salpingella
	Pleuronema glaciale
	Tiarina
	Didinium
	Mesodinium rubrum

1.2.4 Metazoa

The zooplankton community in Ellis Fjord is dominated by small copepods (Kirkwood 1993, Table 1.5). Other zooplankton that are abundant include a hydromedusan, a ctenophore, an appendicularian, a polychaete, and echinoderm pluteus larvae. The community is low in species richness and has a highly variable density that is greatest between late summer and autumn (Kirkwood 1993). A gradient in the zooplankton community composition occurs along the fjord; the community at the seaward end is typical of coastal Antarctic sites, while the community at the landward end shows affinities with communities from the regional saline lakes (Kirkwood 1993). While considerable variability in the zooplankton communities along the fjord has been recorded they all show a similar seasonal cycle (Kirkwood 1993).

Table 1.5. The dominant (>10 m^{-3}) zooplankton taxa in Ellis Fjord (Kirkwood 1993).

Summer 1985/6		Summer 1987/8	
Taxa	No. m^{-3}	Taxa	No. m^{-3}
Oncaea curvata	845	*Oncaea curvata*	920
Fritillaria antarctica	102	*Fritillaria antarctica*	163
Oithona similis	91	Unidentified eggs	80
Unidentified eggs	86	Small nauplii	61
Small nauplii	56	*Paralabidocera antarctica*	56
Callianira cristata	40	Harpacticoida spp	57
Harpacticoida spp.	38	Echinoderm pluteus	30
Ascidiacea larvae	24	Ascidiacea larvae	18
Calanoides acutus	20	*Drepanopus bispinosus*	10
		Oithona similis	10

1.3 Benthic community

The benthos in Ellis Fjord comprises four major substrata: sand, rock, serpulid tubeworm colonies (*Serpula narconensis*), and red alga (*Phyllophora*

antarctica) colonies. The tube worm colonies are the most abundant benthic species in the fjord and form one of the largest known tubeworm reefs in the world (Kirkwood & Burton 1988). An echinoid and limpet species are also reported to be highly abundant. While *Phyllophora antarctica* is the only macrophyte recorded in the fjord, other benthic plant life include mats of benthic diatoms and a coralline alga (Kirkwood & Burton 1988).

1.4 Biogeochemical cycling

1.4.1 Production

Chlorophyll *a* concentration in Ellis Fjord is generally low (<0.15 $\mu g\ L^{-1}$) during winter, but increases during spring and summer with maximum concentrations occurring in the upper 5 m of the water column (Kirkwood 1993, Gibson 1998). There is considerable interannual variation in the magnitude of the chlorophyll maximum during summer ranging from <10 to 30 $\mu g\ L^{-1}$ (Kirkwood 1993, McMinn et al. 1995, Gibson 1998). The highest maximum ever recorded in the fjord, and possibly the highest concentration ever reported in Antarctic waters, was 503 $\mu g\ L^{-1}$ during December 1985 (Kirkwood 1993). This occurred directly beneath the ice in Deep Meromictic Basin and probably resulted from the transmission of high levels of photosynthetically active radiation (PAR) in the water column, due to the transparency of the ice at this site, as well as the summer stratification of the water column (Kirkwood 1993). Ellis Fjord generally supports higher production than that commonly observed in adjacent coastal waters, as a result of the stratification of the water column during summer that maintains much of the biological production in the upper water column (Kirkwood 1993, McMinn et al. 1995). This results in an extended period of production (up to 7 months) in the fjord compared to <2-3 months in other marine Antarctic waters (Krebs 1983, Perrin et al. 1987, Gibson 1998).

1.4.2 Sedimentation

The total annual carbon flux in Ellis Fjord has been reported to be approximately 6.0 $g\ m^{-2}$ (Gibson 1998). This is much lower than that recorded in other Antarctic coastal waters (Karl et al. 1991). However, the seasonal pattern of sedimentation and composition of the sedimenting material in Ellis Fjord appears similar. Fluxes are low in winter and higher in

summer, with maximum rates co-occurring with high phytoplankton production during summer (Gibson 1998). Diatoms, particularly ice-algae, dominate the biomass of settling material during spring and summer, and are an important source of organic carbon (Gibson 1998). Zooplankton faecal pellets and eggs also contribute to biogenic flux throughout summer, while unidentifiable detritus and organic remains, commonly termed 'marine snow', constitute the low flux of organic matter during winter (Gibson 1998). Fluxes of organic carbon appear greatest in near-surface waters and no seasonal patterns in the sedimentation of organic carbon have been observed at depth, which suggests that much of the production in Ellis Fjord is remineralised (Gibson 1998).

Chapter 2

Sediment trap methodology

2.1 Introduction

The enhanced greenhouse effect as a result of anthropogenic CO_2 release has focussed international research on the processes that mediate concentrations of CO_2 in the atmosphere. Vertical flux of carbon to ocean depths is the principal sink for atmospheric CO_2 (Falkowski et al. 1998, Rivkin & Legendre 2001). As a result, sediment traps have become an integral piece of sampling equipment for the study of carbon flux and sequestration in the oceans (Knauer et al. 1984, Bloesch 1988, Lee et al. 1992, Hedges et al. 1993, Bloesch 1996).

Sediment traps were first used in the early 1900s to measure sedimentation rates of particulate matter in lakes, but without much thought given to their design and trapping efficiency (Bloesch 1996). Subsequently, throughout the 1970s, studies of their hydrodynamics were undertaken and by the 1980s it was generally accepted that a simple cylinder with a diameter ≥ 5 cm and an aspect ratio ≥5:1 gave optimal collection of particles (reviewed in Bloesch 1996). There have been few developments on the cylinder design, with most studies focused on modelling hydrodynamic flow around and within traps (Buesseler 1991, Gust et al. 1992, Nodder & Alexander 1999, Tian et al. 2001). However, Rosa et al. (1994) suggested that a funnel connected to a cylinder was useful for harvesting material and did not affect the trapping efficiency. Two designs have also been developed that minimise over-trapping due to the accumulation of otherwise transient swimmers (Coale 1990, Peterson et al. 1993). As traps became used in the oceans, funnel traps were used to maximise the quantity of material collected to compensate for the paucity of settling particles due to high turbulence and low production in the oceans (Honjo et al. 1980, Bloesch 1996). However, funnel traps, particularly those deployed in the upper ocean, still undersampled the flux as a result of high turbulence, and baffles were often added to enhance trapping efficiency (Banse 1990). Thus, in regions of high turbulence and low production, such

as the oceans, funnel traps (often with baffles) are generally used. In regions of low turbulence and high production, such as coastal waters and lakes, the cylinder design is favoured.

Both the sediment trap design and local biogeochemical processes affect the quantity and composition of particles collected (Bloesch & Burns 1980, Peterson et al. 1993, Wakeham et al. 1993). It is generally accepted that to combat degradation and grazing of material collected in traps, they should be treated with a poison or preservative if deployed for >2-3 weeks (Knauer et al. 1984, Gunderson et al. 1990, Lee et al. 1992, Rosa et al. 1994). Despite these findings, Honjo (1996) claimed that poisons may not be required in the polar regions, and numerous sediment trap studies in Antarctic coastal waters have used untreated traps for deployments from a few days to one month (Sasaki & Hoshiai 1986, Fabiano et al. 1997, Matsuda et al. 1987, Cripps & Clarke 1998, Pusceddu et al. 1999, Schloss et al. 1999).

While treatments stop respiration and grazing in traps, leaching of poisons and preservatives can decrease the effectiveness of the treatments (Gardner et al. 1983, Lee et al. 1992, Gardner & Zhang 1997). Furthermore, the effect of turbulence within the trap during retrieval may lead to the loss, or what is often termed 'washout', of material (Lee et al. 1992, Nodder & Alexander 1999). The addition of brine can counter such washout from sediment traps by providing a higher density medium than the surrounding seawater (Gardner & Zhang 1997). However, it was recently reported that the addition of brine can lead to under-trapping by providing a physical boundary to settling material, thereby decreasing the aspect ratio of the trap (Gardner & Zhang 1997, Nodder & Alexander 1999). Consequently, if brine is to assist in the retention of trapped material, the volume of brine should be markedly less than the total volume of the trap so that particles can settle without interference prior to settling across the sea-water / brine interface (Nodder & Alexander 1999). The addition of brine to sediment traps can also induce adverse osmotic effects on the biotic components of settled material and swimmers. For example, the guts of copepod swimmers were reported to protrude outside the body wall leading to spillage of the gut contents (Peterson & Dam 1990).

The accumulation of otherwise transient swimmers can lead to substantial over-trapping and is therefore a considerable problem in treated traps (Knauer et al. 1984, Bloesch 1988, Gunderson 1990, Lee 1990). Attempts to minimise this problem have included the use of baffles, and experimentation with various sediment trap designs to physically exclude or segregate swimmers from other settled material (Coale 1990, Peterson et al. 1993). The simplest methodology that has been generally accepted over the years is to pick swimmers from sedimented material prior to any analyses (Gunderson et al. 1990, Michaels et al. 1990). However, there has been concern that not all swimmers are easily observed, and the identification of smaller metazoans and 'cryptic' gelatinous swimmers requires time-consuming examination of material under the microscope (Michaels et al. 1990).

The decision of whether to treat traps with poisons, preservatives, and / or brine to maximise trapping efficiency is dependent on the intended analyses of the collected material, and the physical and biological characteristics of the site of deployment (Gunderson 1988, Wefer 1989, Honjo 1990, Lee et al. 1992). It has been recommended since the 1970s that treated and untreated traps should be deployed simultaneously to provide an understanding of the reliability of the measured flux (Brock 1978, Knauer et al. 1984, Rosa et al. 1994). Few studies have adopted this approach and I am not aware of any such studies that have been conducted in Antarctic waters.

Most sediment trap studies, including those that have compared the effects of various treatments, have focused on the measurement of chemical properties of the settled material (e.g. Knauer et al. 1984, Wakeham et al. 1993, Khripounoff & Crassous 1994, Cripps & Clarke 1998, Heiskanen et al. 1998). To my knowledge, no studies have compared the physiological response of protists and metazoa to various treatments commonly used in sediment traps, yet much of the settled material is of biotic origin. Since this thesis examines the regulation of flux, it is vital to determine whether my trap methodology created artefacts (defecation, cell lysis, or trapped transient swimmers) that may result in an under- or overestimation of total flux, or changed the contribution by particular taxa to this flux.

In this Chapter I justify the sediment trap design and choice of poison used in the experiments described in this thesis. I then examine the effect of

poisoned and non-poisoned traps on the quantity and composition of settled material over time in light of results from laboratory experiments that investigate the physical response of protistan and metazoan taxa to poison and preservative treatments both with and without the addition of brine.

2.2 Methods

2.2.1 Description of study site

For logistical reasons (ice-conditions, transport of equipment, and availability of personnel) this study was conducted at O'Gorman Rocks, 1 km offshore from Davis station, 68°34.2' S, 77°56.4'E (Figures 2.1a & b). The proximity of this site to the research station has meant that its physical oceanography and biology have been studied intensively over the last decade and, with a few exceptions, the biology at this site is similar to that in Ellis Fjord (Davidson & Marchant 1992, Kirkwood 1993, McMinn & Hodgson 1993, Archer et al. 1996a, Leakey et al. 1996, Gibson 1998, Swadling 1998). The site has a depth of approximately 20 m and is ice-covered in early summer (Gibson 1998). This experiment was conducted from 11 - 20 November 1997, at which time the site had around 1.5 m thickness of ice-cover.

2.2.2 Sampling

Sediment traps were made of poly-vinyl chloride (PVC) which countered the ill-effects of exposure to light, the undesirable leaching of material that would bias chemical analyses, and provided an adequate weight to allow the traps to remain upright when suspended. The traps followed the design described by Bloesch & Burns (1980) and Rosa et al. (1994), consisting of a cylindrical section (internal diameter 65 mm, 6:1 aspect ratio) connected to a funnel that tapered into a cylindrical collector tube (Appendix 1). A total of 24 holes (three rows of eight holes spaced approximately 2 m apart) were drilled through the sea ice using a 20 cm auger attached to a Jiffy drill. A single sediment trap was suspended in each of the holes at a depth of 10 m. The three rows represented three replicate samples. The eight traps in each row consisted of two randomly assigned treatments (poison and non-poisoned) which were left *in situ* for four time periods, either 5, 7, 10, or 14 days. The poisoned traps were filled with 0.2 μm filtered seawater and

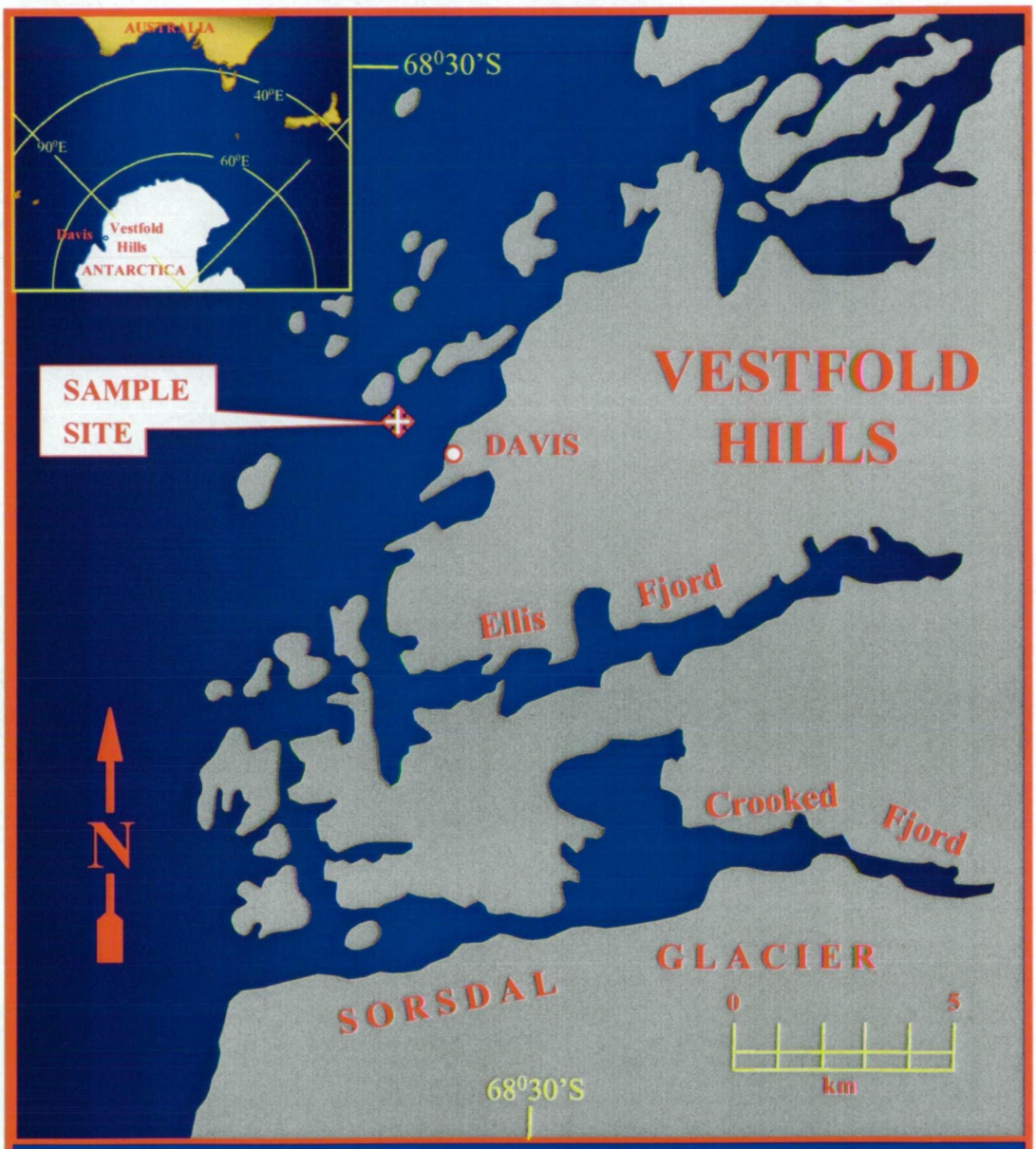


Figure 2.1a. A map of the Vestfold Hills region showing the location of Davis Station and the sampling site at O'Gorman Rocks in relation to the Australian and Antarctic continents.

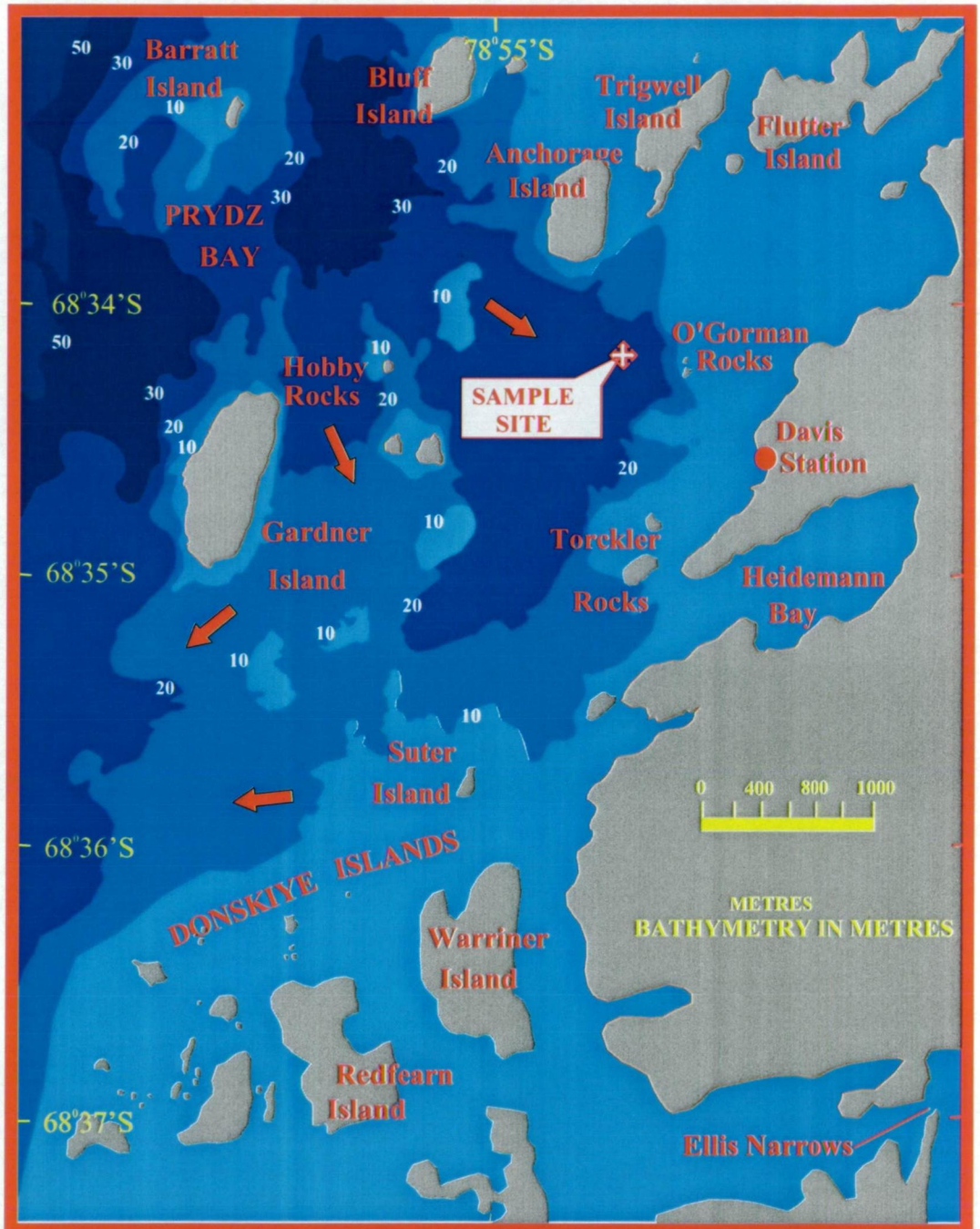


Figure 2.1b. A bathymetric map of the coastal waters off Davis Station showing the location of the sampling Site at O'Gorman Rocks. The arrows indicate the approximate direction of current flow.

mercuric chloride (3.25×10^{-2} g L^{-1}). The non-poisoned traps contained only 0.2 μm filtered seawater. Each of the three replicates of poison and non-poisoned traps were retrieved at each of the time periods (i.e. 6 traps were retrieved at 5, 7, 10 and 14 days). The collector tubes were capped and samples were placed in a dark, insulated container, and transported to the laboratory at Davis station.

2.2.3 Sediment trap analyses

In the laboratory, the sediment trap sample was mixed, then sub-sampled for several analyses: 10 ml was used for the determination of bacterioplankton concentration; 10 ml for identity and concentration of protists, metazoa and faecal pellets; and, 80 ml each for the analysis of total particulate organic carbon (POC) and dry weight of trapped material.

2.2.3.1 Bacterioplankton

Samples were immediately stored in 2% glutaraldehyde and later filter-concentrated to approximately 2 ml in a 25 mm diameter filtration apparatus fitted with 0.2 μm pore size black polycarbonate membrane filters (Poretics). Sixty μl of 500 μg/ml solution of 4', 6-diamino-2-phenolindole (DAPI) (Sigma) in MilliQ water was added to the concentrates. The samples were mixed, placed in the dark for 15 minutes, filtered to dryness and mounted on slides. Bacteria were counted over 20 replicate fields at 1000 x magnification using UV epifluorescence on a Zeiss Axiovert microscope.

2.2.3.2 Protists, metazoa and faecal pellets

Samples were transferred to a glass, capped container, fixed with acidified Lugol's iodine, and refrigerated at 0-4°C prior to microscopic analysis. Metazoa were removed from the sample and identified and counted using a dissecting microscope. Protists were settled in Utermöhl sedimenting chambers, identified and counted at 400 x magnification using phase contrast optics on a Leitz Fluovert inverted microscope. For the majority of samples, the entire sample was counted. However, where protists were in high concentration, fifteen replicate fields were counted per sample, as this was shown to reduce the variance between fields and provide a reliable estimate of the mean, and the mean and standard error calculated. Dominant protist

taxa were identified to species where possible and to genus or class where light microscopy did not allow detailed identification. Faecal pellet identity and concentration was determined for the entire sample.

2.2.3.3 Particulate organic carbon

Filtration glassware, filters and forceps were combusted in a muffle furnace at 525°C for ≥24 hours. If no algal mat material was present, the sample was passed through a 200 μm mesh to remove any metazoan swimmers. Otherwise, swimmers were picked from the sample by observation with the naked eye. The sample was then filtered onto a pre-weighed Whatman GF/F filter. Filters were folded in half, placed in clean plastic bags, sealed and weighed to $\pm 1.0 \times 10^{-5}$ g. The samples were then frozen at – 20°C for later analysis.

A modified plastic syringe that had been soaked in 10% Decon 90® at 60°C for ≥12 hours and rinsed thoroughly with Milli Q water was used to punch a 2.69 mm diameter hole in the folded filter resulting in a double punch of the sample. Blank filter samples were similarly prepared. The syringes containing the punched sample were fumed in an acid bath for ≥24 h, then oven dried at 60°C for ≥24 h. Samples were placed in pre-cleaned, ultra light-weight, pressed tin capsules (5 x 8 mm) that were crushed into a cube to expel excess air, and subsequently run using a Carlo Erba Elemental Analyser at the Central Science Laboratories, University of Tasmania.

2.2.3.4 Dry weight

Each sample was filtered onto a pre-weighed nucleopore filter, dried at 60°C for ≥24 h, and weighed to $\pm 1.0 \times 10^{-5}$ g. The filter was subsequently dried again and re-weighed to verify the mass recorded.

2.2.3.5 Statistics

A single factor analysis of variance (ANOVA) was performed using STATISTICA© 6.0 (Statsoft Inc. 2001). This examined the effects of time (independent variable) on the flux (m^{-2} day^{-1}) of a single parameter e.g. bacteria (dependent variable). This was performed for all parameters measured from both treated and untreated traps (i.e. a total of 12 ANOVAs were performed). The probability of the F statistic was used to determine the

significance of effects (at $\alpha = 0.05$). No analysis was undertaken for the phytoplankton as the samples between replicates were not directly comparable. This resulted from the very high concentration in traps on Day 10 in untreated traps, and Days 10 & 14 in treated traps, which precluded counting the entire sample, and therefore 15 replicate fields were counted for samples obtained on these days (see 2.2.3.2 Protists, metazoa and faecal pellets).

2.2.4 Effect of poisons and preservatives

2.2.4.1 Protists

Five individual cultures of Antarctic protists were obtained: a diatom (*Fragilariopsis* sp.) a phytoflagellate (*Pyramimonas* sp.), an autotrophic dinoflagellate (*Polarella glacialis*), an unidentified heterotrophic nanoflagellate, and an unidentified heterotrophic dinoflagellate. The live cultures were first examined at 400 x magnification using Nomarski optics on a Zeiss Axiovert microscope to ensure the cultures contained healthy cells. A sample of each of the cultures was pipetted into three replicate samples of four treatments: 1) mercuric chloride (0.0325 g L^{-1}) in brine (50 g L^{-1}), 2) mercuric chloride in 0.2 μm filtered sea-water, 3) glutaraldehyde (4%) in brine and, 4) glutaraldehyde in 0.2 μm filtered sea-water. Glutaraldehyde is a standard fixative for protists that has a minimal effect on cell morphology and ultrastructure (Hayat 1989), and was therefore used as a 'control' in this experiment. Brine is often added to sediment traps to minimise loss of material during retrieval, therefore the effect of brine in conjunction with poisons and preservatives was also investigated.

Samples were prepared in Utermöhl chambers and allowed to settle for ≥24 hours. Five microscope fields from each replicate sample were counted and cells were classified as either 1) intact, 2) vesicularised, where cells had intra- and extracellular vesicles extruding through the plasmalemma, or 3) burst. Replicate counts were pooled to provide fifteen replicate fields per treatment (see 2.2.3.2 Protists, metazoa and faecal pellets). Samples were stored at 0-4 °C, re-examined after one week, and five fields counted from one replicate of each treatment. To remove the bias of varying concentrations between species, the data were converted to the proportion intact, vesicularised, or burst. The proportion data were then normalised prior to the analysis of variance using the arcsine transformation, which accounts for the large

number of zero values that have zero variance in the data (Zar 1984). To investigate the effect of the treatment on cell physiology, a General Linear Model (GLM) was used to perform a MANOVA, which allows for the analysis of multiple independent and dependent variables, using STATISTICA© 6.0 (Statsoft Inc. 2001). The species and treatments represented the independent variables and the physiological condition of the cells (intact, vesicularised, or burst) for each species represented the dependent variables. The effects of the treatments on species morphology were also examined after one week and the data were also arcsine transformed to enable calculation of the upper and lower 95% confidence limits about the means.

2.2.4.2 Copepods

A culture of temperate harpacticoid copepods was used in the experiments. Twenty copepods were double-picked into petri dishes of 0.2 μm filtered sea-water to ensure they were free of algae. The copepods were then transferred to one of five different treatments in 100 ml beakers and their behaviour monitored using a dissecting microscope. The treatments were: 1) mercuric chloride (0.0325g L^{-1}) in brine (50 g L^{-1}), 2) mercuric chloride, 3) formalin (10%) in brine, 4) formalin, and 5) brine. Formalin is commonly used in sediment trap studies and therefore provided the 'control', while brine was added for the reasons outlined above. The treatments were repeated three times to provide three independent replicate samples. Samples were left to settle for ≥24 h and the supernatant removed by aspiration. The remaining sample was settled in a Utermöhl chamber and examined at 200 x magnification, or 400 x magnification when faecal pellets or protists were observed, using a Zeiss Axoivert inverted microscope. The morphological condition of the copepods was noted, faecal pellets and protists counted, and the mean and standard error of the three replicate samples calculated. Samples were stored at 0-4 °C and and re-examined after one week.

2.3 Results

2.3.1 Sediment traps

2.3.1.1 Phytoplankton and bacteria

The flux of bacteria in both treated and untreated traps showed highly significant changes over time (Table 2.1). Most notably there was a rapid

increase in flux in non-poisoned traps and a slight decrease in flux in poisoned traps after seven days (Figure 2.2a). Phytoplankton flux was initially low in non-poisoned traps, increasing between 7 and 10 days, but declined by approximately 70% between 10 & 14 days (Figure 2.2b). In poisoned traps the flux of phytoplankton rapidly increased after 7 days and was then maintained (Figure 2.2b).

Table 2.1. Significant changes in flux rate (m^{-2} day^{-1}) with time in poisoned and non-poisoned traps. P values: * <.05, ** <.01, *** <.001, n.s. = not significant

	Poison			Non-Poison		
	df	F value	P	df	F value	P
Bacteria	1, 219	13.40	***	1, 239	44.12	***
Protozoa	1, 10	0.53	n.s.	1, 9	3.96	n.s.
Copepods	1, 10	0.37	n.s	1, 9	0.52	n.s.
Faecal pellets	1, 11	0.31	n.s	1, 9	0.85	n.s.
POC	1, 11	0.96	n.s	1, 8	0.053	n.s.
Dry weight	1, 11	10.69	**	1, 11	5.85	*

2.3.1.2 Microheterotrophs

The flux of protozoa was similar in both the poisoned and non-poisoned traps, although flux tended to be greater in the non-poisoned traps particularly after 10 days (Figure 2.2c). However, overall the flux of protozoa in both poisoned and non-poisoned traps did not change significantly (Table 2.1). Similarly, there were no significant changes in copepod flux over time, although flux was generally greater in poisoned traps (Figure 2.2d, Table 2.1).

2.3.1.3 Faecal pellets, POC and dry weight

The flux of faecal pellets in both poisoned and non-poisoned traps did not change significantly over time (Table 2.1). Faecal pellet flux was greater in the poisoned traps in the first 7 days, but after 7 days there was greater flux in the non-poisoned traps (Figure 2.3a). Similarly, the flux of POC in

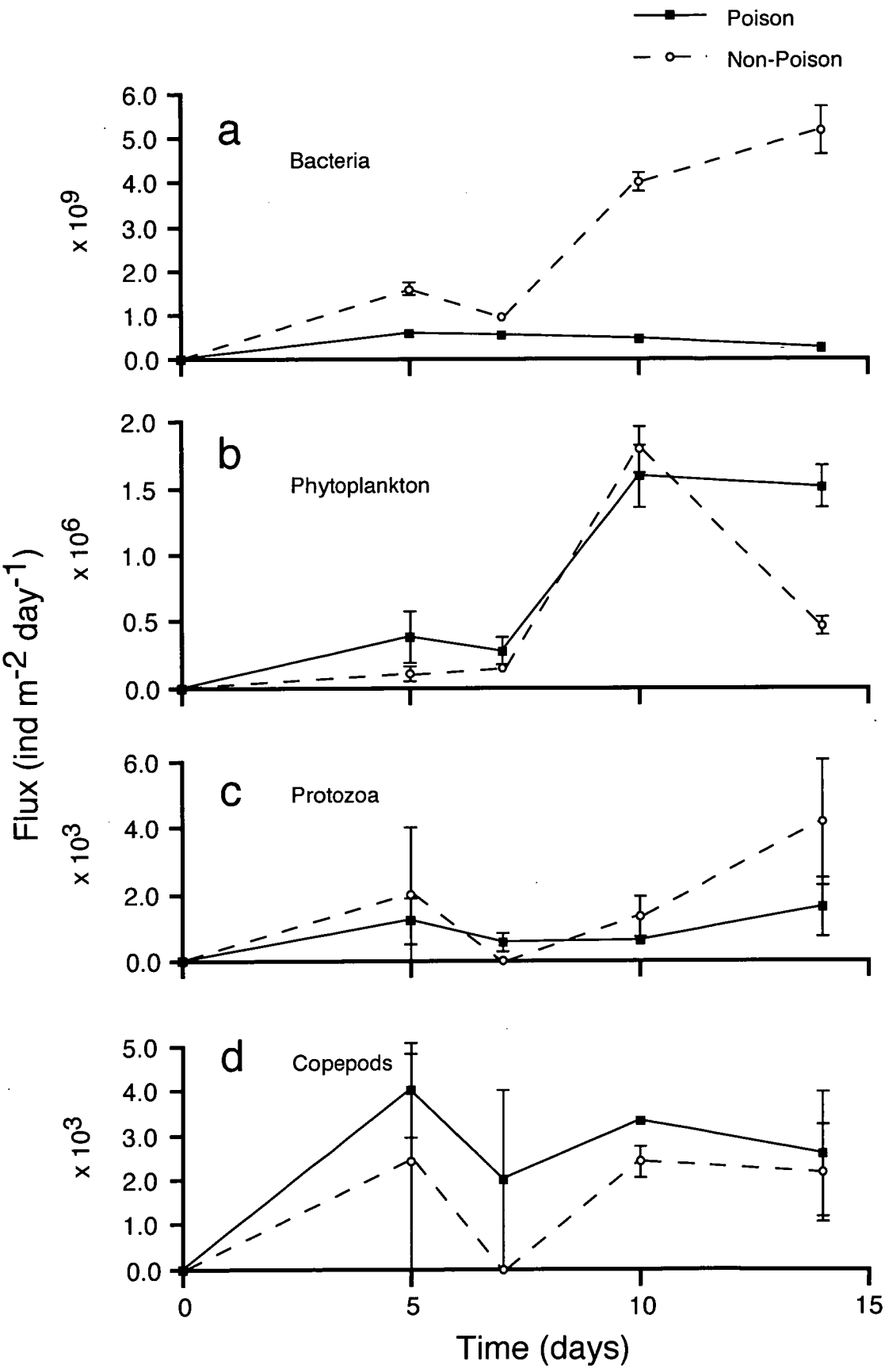


Figure 2.2. Flux rate of a) bacteria, b) phytoplankton, c) protozoa, and d) copepods into sediment traps over 14 days. Mean ± SE (n = 3)

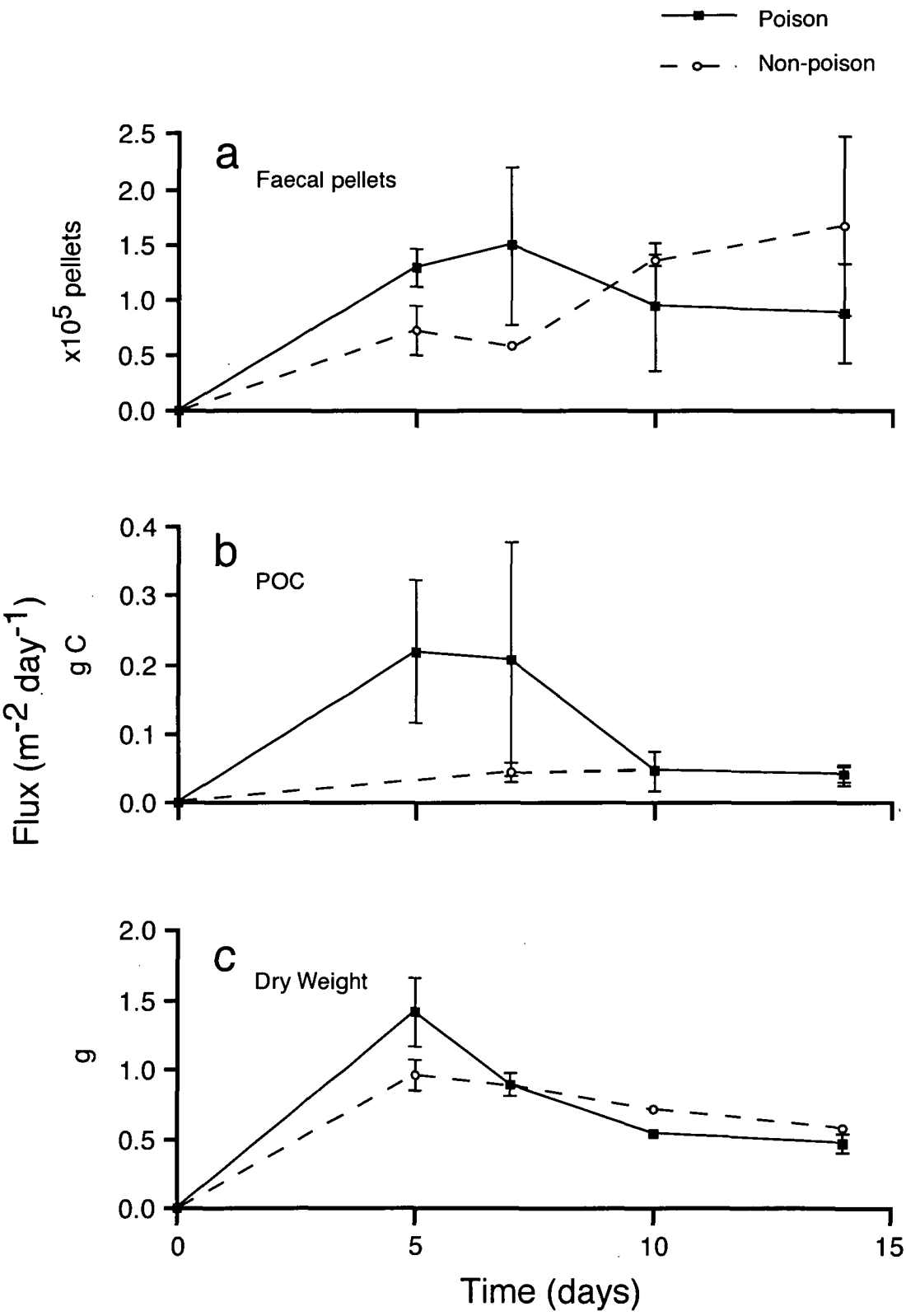


Figure 2.3. Flux rate of a) faecal pellets, b) particulate organic carbon, and c) dry weight collected in sediment traps over 14 days. Mean ± SE (n = 3)

poisoned traps was highest during the first 7 days and declined thereafter (Figure 2.3b). In contrast, the flux of POC in non-poisoned traps remained relatively constant. POC flux did not change significantly during the experiment. However, the overall mass of settled material did change significantly in both poisoned and non-poisoned traps, with the highest flux occurring during the first 5 days (Figure 2.3c).

2.3.2 Effect of poisons and preservatives on protists and copepods

2.3.2.1 Protists

All treatments caused mortality of all cells. Most cells became larger and more distorted in the mercuric chloride treatments compared to those in the control treatments (glutaraldehyde). Overall, there was a high proportion of vesicularised cells compared to the control treatments, but a low proportion of burst cells (Figures 2.4a, c, & e). This was reflected statistically as highly significant differences were observed in the number of intact and vesicularised cells between the treatments and the control but there were few significant differences between the number of burst cells (Figures 2.4b, d, & f)). The autotrophic dinoflagellate *Polarella* sp. and the diatom *Fragilariopsis* sp. were least affected by the treatments, while the heterotrophic taxa (dinoflagellates and nanoflagellates) were most affected, showing a significantly greater number of burst cells between the treatments and the controls. The addition of brine to glutaraldehyde treatments had no significant effect on cell morphology, however significant effects were observed between the mercuric chloride treatments with and without brine (Figures 2.4a-f). In the absence of brine, diatoms cells showed slightly more intracellular vesicularisation due to mercuric chloride, and there was a significantly greater proportion of burst heterotrophic dinoflagellate cells.

After one week there was no significant change in the morphological appearance of cells for all taxa and treatments (Appendix 2). The exception was *Pyramimonas* sp. that appeared to have more intact cells in the glutaraldehyde and brine treatment and less vesicularised cells in the glutaraldehyde treatments with and without brine. These anomalous results are likely due to the variability between replicates. While three replicate samples were counted in the initial experiment, only one replicate sample was re-counted one week later.

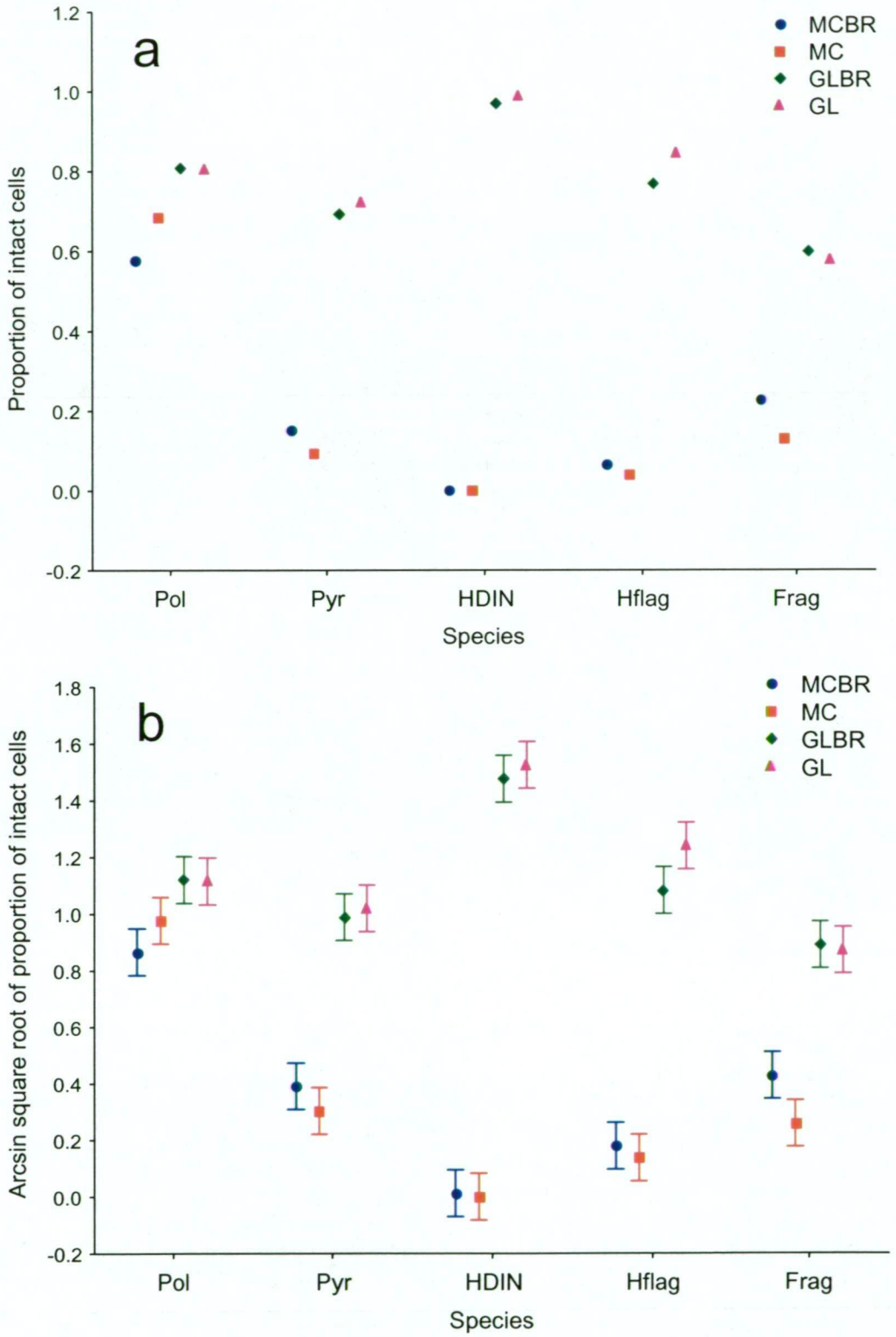


Figure 2.4. The effect of treatment on the morphological state of individual species / taxa, shows a) the proportion of intact cells, and b) the transformed proportion showing the error bars that represent the 95% confidence intervals. Pol = *Polarella* sp., Pyr = *Pyramimonas* sp., HDIN = heterotrophic dinoflagellate, Hflag = heterotrophic flagellate, Frag = *Fragillariopsis* sp. MCBR = mercuric chloride and brine, MC = mercuric chloride, GLBR = glutaraldehyde and brine, GL = glutaraldehyde.

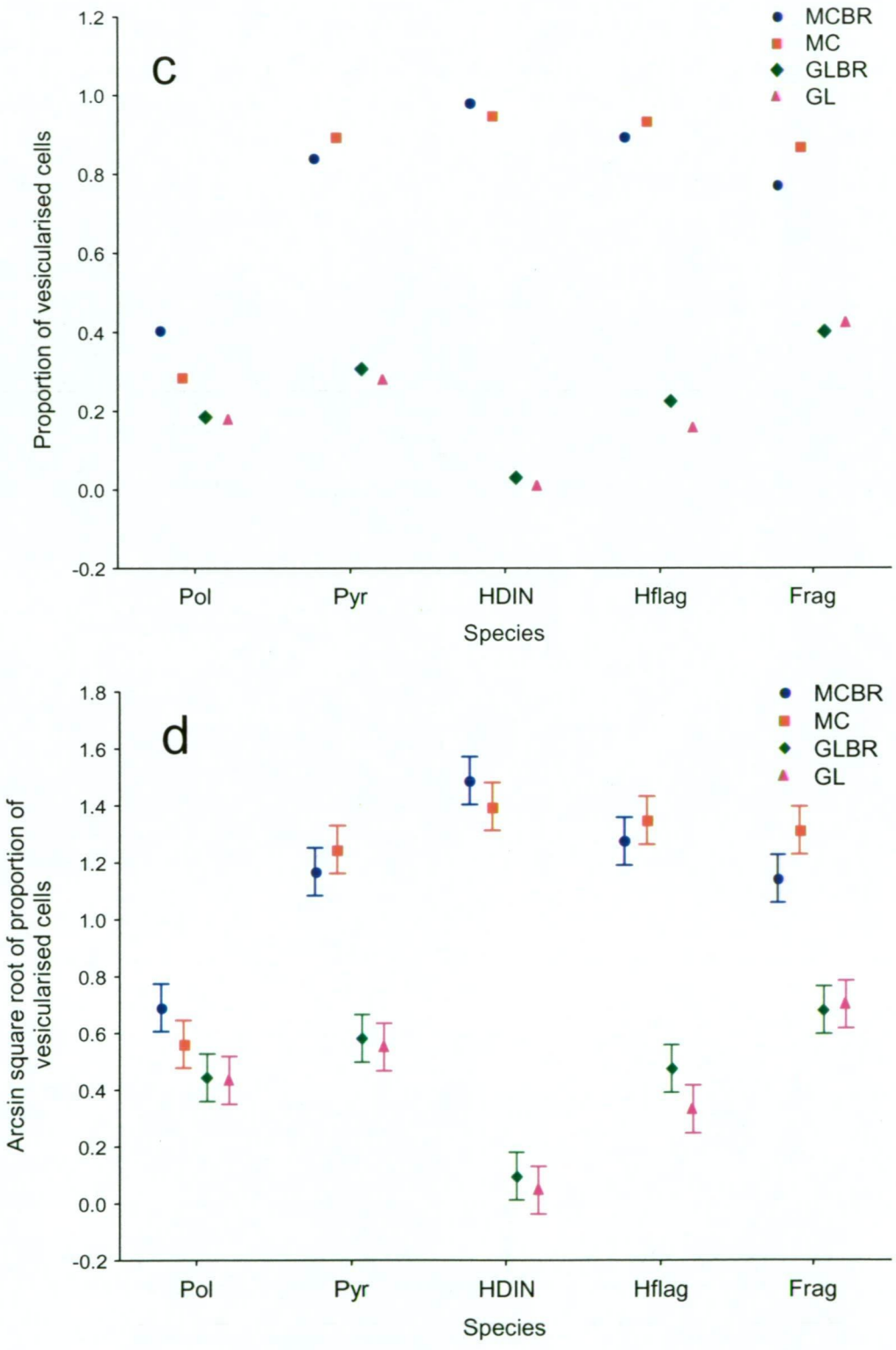


Figure 2.4. The effect of treatment on the morphological state of individual species / taxa, shows c) the proportion of vesicularised cells, and d) the transformed proportion showing the error bars that represent the 95% confidence intervals. Pol = *Polarella* sp., Pyr = *Pyramimonas* sp., HDIN = heterotrophic dinoflagellate, Hflag = heterotrophic flagellate, Frag = *Fragillariopsis* sp. MCBR = mercuric chloride and brine, MC = mercuric chloride, GLBR = glutaraldehyde and brine, GL = glutaraldehyde.

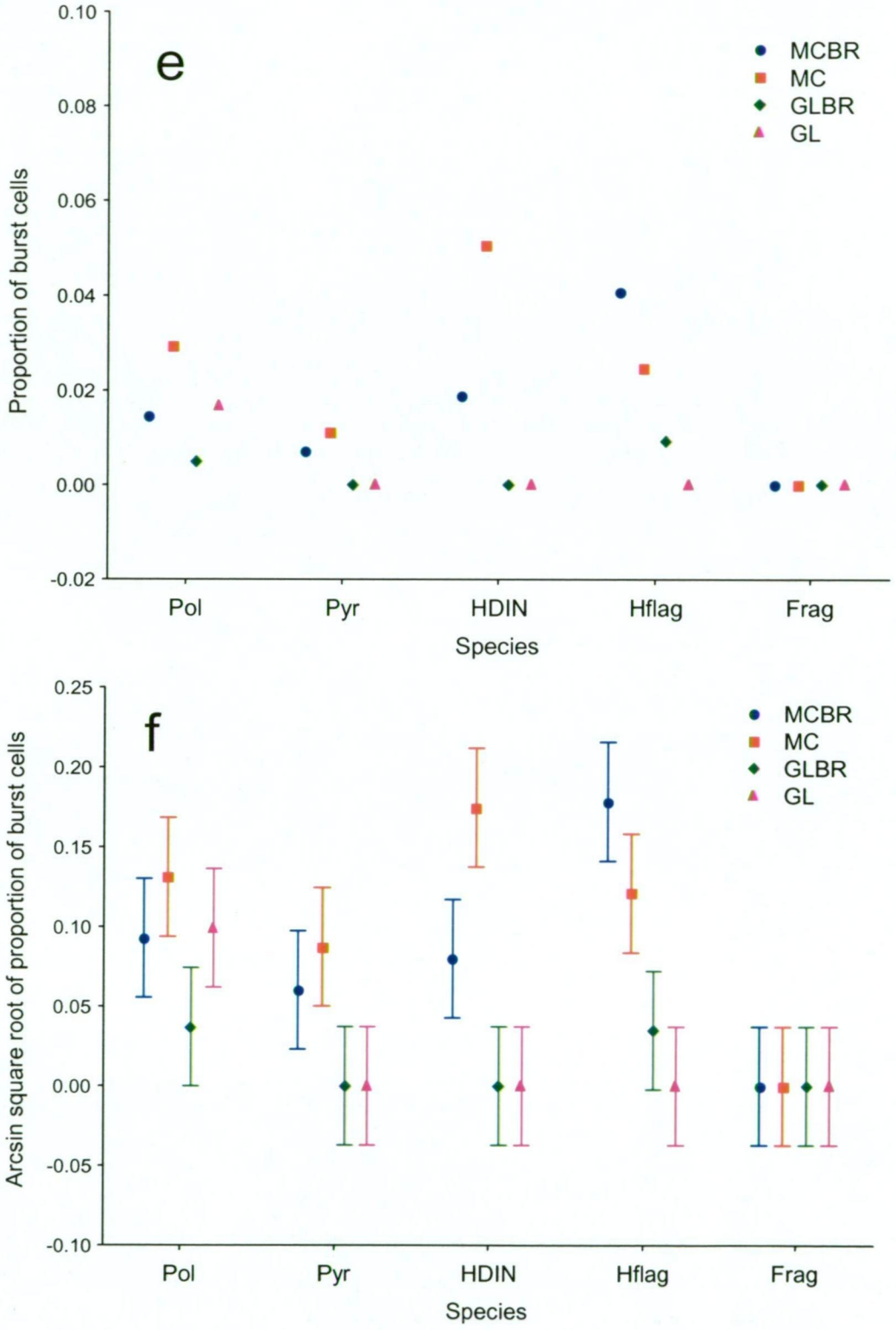


Figure 2.4. The effect of treatment on the morphological state of individual species / taxa, shows e) the proportion of burst cells, and f) the transformed proportion showing the error bars that represent the 95% confidence intervals. Pol = *Polarella* sp., Pyr = *Pyramimonas* sp., HDIN = heterotrophic dinoflagellate, Hflag = heterotrophic flagellate, Frag = *Fragillariopsis* sp. MCBR = mercuric chloride and brine, MC = mercuric chloride, GLBR = glutaraldehyde and brine, GL = glutaraldehyde.

2.3.2.2 Copepods

Differences in the time taken for copepods to die were observed between treatments. The copepods subjected to mercuric chloride and brine solution stopped swimming after 1-2 minutes, although their antennae remained moving for up to 5 minutes before they died. Copepods that were subjected to only mercuric chloride (no brine) remained swimming for up to 5 minutes, while a small proportion (around 20%) were still swimming after 10 minutes. All copepods died after 15-20 minutes. Copepods died instantly in formalin treatments with and without brine. In the brine treatment without poison or preservative, copepods ceased swimming after 1 minute, however their antennae remained moving for 10-15 minutes and all had died after 20-30 minutes.

None of the treatments appeared to affect copepod morphology and all bodies remained intact. However, there was discolouration of the body tissue and some detachment of egg sacs in the formalin treatments, while the bodies appeared pale in the brine-only treatments. No protists were observed in the samples. Faecal pellets were observed in all treatments, although the formalin fixed treatment contained significantly fewer faecal pellets than other treatments (Table 2.2). There was no detectable difference in the morphology of copepods killed using mercuric chloride or formalin, and the entire copepods could be picked without disintegrating after one week. In contrast, in the brine only treatment, most bodies had suffered varying stages of degradation, appeared semi-transparent, and often only the cephalosome remained.

Table 2.2. Mean number of faecal pellets in treated samples. n = 3

Treatment	Mean	SE
Mercuric chloride & Brine	3.33	0.67
Mercuric chloride	3.33	0.33
Formalin & Brine	3.67	0.88
Formalin	1.33	0.67
Brine	4.00	1.15

2.4 Discussion

2.4.1 Sediment trap design and poisons

The sediment trap design used in this study was chosen in accordance with the accepted cylindrical design for coastal waters. In addition, the traps were designed to maximise trapping efficiency, and to be simple (to minimise complications in a remote field environment), of low cost, and of a suitable size that could be deployed through a 20 cm ice-hole by a single operator. The traps had an aspect ratio, based only on the cylinder section of the trap, of 6:1, but the funnel would have led to an aspect ratio >10:1. These aspect ratios reportedly result in retention rates between 103% and 97%, respectively, during periods of low turbulence (Bloesch & Burns 1980 as modified in Rosa et al. 1994). During the set-up of my experiments in Ellis Fjord (see Chapters 3-6), I attempted to measure current speeds using a flowmeter, but problems with ice (clogging of the meter) and the stability of the vane, rendered the data unreliable. High flow rates have been recorded through the narrow seaward entrance to the fjord where the ice often melts completely during summer leaving this entrance exposed to wind-induced turbulence (Kirkwood 1993). However, the flow rate at the landward entrance is low and the ice rarely melts completely. My study site was located towards the landward end of the fjord and remained ice-covered throughout summer, suggesting that turbulence was likely to be low during this study.

In this study, and at the main study site of Ellis Fjord, a single sediment trap was deployed in each hole. Sediment trap deployments often consist of an array of traps suspended on a single line at different depths. This can result in between-trap interactions that can compromise the trapping efficiency (Nodder & Alexander 1999). My traps were spaced around 2 m apart, minimising between-trap interactions. In addition, the replicate traps would have provided an indication of the high spatial variability inherent under ice-cover.

Mercuric chloride was used in this study to kill biotic material, minimise respiration and grazing, and allow measurement of POC. The main treatments that have been used in sediment traps are formalin, sodium azide

and mercuric chloride. Formalin can interfere with carbon measurements, and sodium azide is reportedly less effective in retarding microbial activity (Knauer et al. 1984, Lee et al. 1992). Mercuric chloride is effective at stopping microbial decomposition at low concentration (≤50 mg L^{-1}) and diffuses slowly (Knauer et al. 1984, Lee et al. 1992, Honjo 1996). A concentration of 32.5 mg L^{-1} $HgCl_2$ used in this study reduced microbial activity and caused protistan and metazoan mortality in both the laboratory and field (see below). In addition, observations during trap deployments suggested that suspension of material from the collector tube into the body of the trap and washout of material from traps during retrieval may have been substantial. The addition of brine to only the collector tube would assist in retention of material without compromising the aspect ratio of the trap as the volume of the tube is much smaller than the total volume of the trap.

2.4.2 Trap treatments

The aim of using poisons or preservatives and brine in traps is to maximise trapping efficiency (Wakeham et al. 1993). Below, I interpret results from laboratory and field experiments that investigate taxa-specific responses to poisons, preservatives, and brine, and the degree of under- and over-trapping in treated and untreated traps.

2.4.2.1 Untreated traps

Respiration of sedimented material by bacterioplankton is one of the primary causes of degradation of matter in untreated traps (Gardner et al. 1983, Taylor et al. 1986, Gunderson 1988, Gunderson et al. 1990). Studies have reported rates of decay of organic matter as high as 1% per day, and up to a 60% decrease in total organic carbon (TOC) flux due to microbial decomposition (Gardner et al. 1983, Naes 1988). However, it has been suggested that at low temperatures, where the rate of degradation is presumed to be low, untreated traps may be deployed for up to 3 weeks without significant microbial decomposition of trapped material (reviewed in Rosa et al. 1994). I found significant changes in the flux of bacteria in untreated traps, particularly after 7 days, suggesting substantial growth and respiration by bacteria in waters at < 0°C. These results support the view that the rate of degradation is dependent upon the composition of the trapped material and the nature of available substrates rather than just temperature,

and that degradation is greater in long-term trap deployments (Gardner et al. 1983, Billen & Becquevort 1991).

While no statistical analyses were performed, a substantial increase in phytoplankton flux was observed between 7 and 10 days. This high flux was not maintained, and the rapid decline in flux after 10 days coincided with a high flux of bacteria, suggesting that respiration may have contributed to decreased phytoplankton flux in untreated traps. Other factors that could have contributed to this decline are phytoplankton cell lysis due to a lack of light in the collector tube, and grazing by proto- and metazoan swimmers.

Swimmers are attracted to the 'organic oasis' of nutrition in sediment traps (Gardner et al. 1983). In the present study, both protozoa and copepods were present in untreated traps. However, there were no significant changes in the flux of these microzooplankton over time. The concentration of microzooplankton in traps was low, which may have resulted from this experiment being conducted during late spring prior to the summer period of peak production. The low concentration of microzooplankton resulted in a small sample size reflected by the low degrees of freedom. A small sample size increases the probability of Type I and II errors (Zar 1984). In this case, a Type I error may have occurred: there may have been significant changes in the concentration of microzooplankton in traps over time but any changes were obscured by the low sample size.

The plot of the mean fluxes of microzooplankton showed that the flux of protozoa increased after 7 days, and continued to increase between 10 and 14 days. This coincided with the decreased flux of phytoplankton and an increased flux of faecal pellets, suggesting that substantial grazing had occurred within the traps. Grazing by swimmers could also have contributed to the high flux of bacteria at this time, as bacteria are attracted to exudates that are released by 'sloppy' feeding (Lampert 1978, Roy et al. 1989, Strom et al. 1997). Therefore, similar to studies in temperate waters, this study indicates that respiration and grazing in untreated traps can result in significant changes in both the quantity and composition of settled material (Harbison & Gilmer 1986, Taylor et al. 1986, Banse 1990).

2.4.2.2 Treated traps

Protists

The types of poisons and preservatives used in sediment traps are chosen to accommodate a range of analyses of settled material, and therefore may not be optimal for maintaining the integrity of all the biotic components. It has been recognised that preservation of protist cells can lead to cell lysis and changes in cell volume that bias estimates of protistan biomass (Sherr & Sherr 1993, Leakey et al. 1994, Menden-Deuer et al. 2001). To my knowledge, only one study has investigated the effect of mercuric chloride on protists. Pace & Orcutt (1981) found that mercuric chloride was an excellent preservative (comparable to Lugol's iodine) for freshwater protozoa.

In the present study mercuric chloride did not cause significant lysis of most protist cells, as the absolute concentration of many protists was not significantly reduced in treated traps. The exceptions were heterotrophic dinoflagellate and nanoflagellate cells that showed significantly greater lysis in mercuric chloride than the controls and may have contributed to under-trapping. However, the effects observed in the laboratory represent the most extreme scenario as cells were immediately exposed to the full concentration of the poison, whereas in sediment traps deployed in the field, cells would have settled through a concentration gradient.

While cell lysis appeared minimal in mercuric chloride treatments, most cells showed varying degrees of vesicularisation that resulted in an increased cell volume. Such changes in cell volume could affect estimates of protist biomass in this thesis (see Chapter 6). However, in general, cells observed in trap material did not appear as vesicularised as those observed in laboratory experiments. There were no additional changes in cell morphology after 1 week, suggesting minimal further deterioration in sediment trap deployments that were generally sampled weekly.

Swimmer biomass

Swimmers can reportedly bias flux estimates by contributing between 7-53% of total POC flux (Steinberg et al. 1998). Consequently, swimmers may present a problem of equal magnitude to degradation for the accurate estimation of flux (Hargrave et al. 1989, Lee et al. 1992, Hedges et al. 1993).

Like that observed in untreated traps, the biomass of swimmers in treated traps did not change significantly over time, and this was likely due to the low sample size (see 2.4.2.1 Untreated traps). While the flux of protozoa was lower and did not change over time in treated traps, the flux of copepods was greater than in untreated traps, suggesting that the accumulation of swimmer biomass may have been significant. Copepods were the only metazoan swimmers observed in trap material in this study and could therefore be picked by observation with the naked eye. While copepods are the most abundant metazoans in Ellis Fjord (see Chapter 3), 'cryptic' swimmers such as larvaceans and ctenophores could be missed without microscopic examination, potentially leading to an overestimation of POC flux. However, larvaceans were not abundant during the summer. While ctenophores could have gone undetected, none were observed in sub-samples from traps. Although the contribution by naturally sinking swimmers to total POC flux appeared minimal, the picking of all swimmers may bias flux estimates due to the removal of swimmers that had suffered natural mortality and moults that would settle in traps (Steinberg et al. 1998).

The use of poisons rather than preservatives in traps may lead to the disintegration of swimmers. Mercuric chloride has been reported to soften the bodies of swimmers (Knauer et al. 1984). However, in this study, mercuric chloride had no effect on the morphology of copepods in the laboratory, and after storage in the poison for one week all copepods could be picked without disintegrating.

Swimmer behaviour

The degree of bias due to swimmers is dependent on their behaviour, as different swimmers are likely to have different responses to various treatments (Harbison & Gilmer 1986, Lee et al. 1992). It has been reported that on contact with poisons, swimmers may void their guts (regurgitation or excretion) leading to over-estimation of settled material (Harbison & Gilmer 1986). To my knowledge, no other studies have investigated the effect of mercuric chloride on copepods. This study showed that mercuric chloride did not cause copepods to evacuate their guts. While significantly fewer faecal pellets were observed in the formalin treatment, there was no significant difference in the number of pellets in the mercuric chloride treatments and formalin with brine. Therefore, excretion by swimmers

within traps was likely to be low. I acknowledge that the copepods used in this experiment were of temperate origin and differences in behaviour may exist between temperate and Antarctic species. Results from this study showed that mercuric chloride, in the absence of brine, did not cause instant mortality of copepods. Therefore, excretion due to grazing by swimmers, rather than gut evacuation induced by poison, probably caused the initially high flux of faecal pellets observed in poisoned traps.

2.4.3 Brine and treatments

2.4.3.1 Protists

The addition of brine to sediment traps may induce adverse osmotic effects leading to bursting and disintegration of protist cells (Hayat 1989). However, this was not observed in the present study, as there was no significant difference in the proportion of burst cells between the mercuric chloride treatments with and without brine. Rather, the addition of brine to mercuric chloride appeared to assist in the preservation of some taxa, as the proportion of lysed cells of heterotrophic dinoflagellates decreased significantly in the presence of brine, and diatom cells suffered slightly less vesicularisation. No significant effect was observed with the addition of brine to glutaraldehyde. This is presumably because the preservative causes instant mortality and fixes body tissues immediately, whereas the poison acts more slowly to cause mortality, and therefore cells are still subject to physicochemical changes.

2.4.3.2 Copepods

The addition of brine to mercuric chloride increased the effectiveness of this poison on temperate copepods in the laboratory and did not have any adverse effects on their morphology. This is undoubtedly influenced by the salinity tolerance of the copepod species, and brine may have no impact on some coastal Antarctic species, such as *Paralabidocera antarctica*, which are capable of living in the brine channels of fast-ice. However, the effect of brine on oceanic species such as *Oithona similis* and *Oncaea curvata* may be similar to that observed in temperate copepods in this study. As mentioned above, the degree of bias due to swimmers is dependent on swimmer behaviour and species-specific responses to the chosen treatment (Harbison & Gilmer 1986,

Lee et al. 1992). It has been suggested that an ideal poison would prevent microbial activity and preserve organic matter collected in the traps while deterring live zooplankton (Working group 2 1988, Gunderson & Wassmann 1990, Lee et al. 1992). I suggest that determination of the salinity tolerance of dominant swimmers may lead to the use of effective concentrations of brine being used as a simple deterrent to swimmers entering sediment traps, particularly at long-term monitoring sites where the occurrence and behaviour of dominant swimmers is known. Overall, more research is required on swimmer behaviour in relation to trapping, poison, and brine to alleviate over-trapping.

2.4.3.3 POC and mass

Despite substantial changes in the composition of settled material over time in untreated traps, there was no significant change in the flux of POC. However, Rivkin et al. (1996) reported that biogenic carbon flux can be independent of food web structure and trophic mode. The lack of change in POC flux I observed may be due to a balance of the loss of carbon by grazing and washout, against an increase in carbon due to the production of faecal pellets.

In treated traps, the flux of POC also did not change significantly. However, the highest flux was observed in the first 5 days. The flux of faecal pellets was also high at this time, and may have contributed to the high POC flux. However, POC flux declined after 7 days despite an increased flux of phytoplankton. This decline in poisoned traps may have been due to washout of material.

A significant change in the mass flux of material was observed, with decreases in both treated and untreated traps over time. This may represent substantial grazing and washout in traps, and also decomposition of material in untreated traps. However, it is also likely to have resulted from changes in the quantity of inorganic material collected in traps. Mineral particles were observed in traps and resuspension of sediments is reportedly common in traps deployed in shallow waters (Rosa et al. 1994, Bloesch 1995, Schloss et al. 1999). In addition, wind-blown particles from the soil and rock that comprise the Vestfold Hills could have entered the traps directly, or via their

entrapment in the overlying snow and ice and subsequent release into the water column.

2.5 Summary of methodology used in this thesis

To maximise the trapping efficiency of the traps deployed in Ellis Fjord, and for the study of the regulation of carbon flux in this thesis, the following methodology was employed:

- A cylindrical sediment trap design (that had a funnel to aid in the collection of material) of an appropriate aspect ratio (6:1) was used to maximise trapping efficiency according to hydrodynamic principles.
- The spatial sampling design alleviated between-trap interactions and took into consideration the high spatial variability of water column processes under ice-cover.
- A sampling period of 7 days was determined to be appropriate, as trap-induced changes in fluxes of material were most marked following >7 days, and this was the shortest sampling period that was logistically feasible.
- Mercuric chloride was chosen as an effective treatment to minimise decomposition of trap material and did not interfere with carbon measurements. It was used to alleviate changes in the composition of material due to grazing and decomposition in non-poisoned traps that increased with the duration of deployment.
- Possible problems of over-trapping of swimmers in poisoned traps were minimised by picking all metazoans ≥500 μm in subsequent laboratory analyses. This was assumed to effectively eliminate the majority of swimmers, as 'cryptic' swimmers were either not abundant at the study site or were not observed in trap material.
- Brine was added to traps to alleviate loss of material due to washout.
- Mercuric chloride had minimal effects on the morphology of protists that comprised most of the material in traps. The addition of brine did not adversely affect material but assisted in the preservation of some protist taxa.

Chapter 3

Phytoplankton - protozoa - metazoa succession and interactions

3.1 Introduction

Knowledge of plankton community structure and trophic processes is required to understand carbon transfer and flux in the ocean (Fenchel 1988, Longhurst 1991, Verity & Smetacek 1996, Wassmann 1998). However, the role of the physical environment and species life-history strategies in determining community structure and trophodynamics has not been adequately studied. Furthermore, little is known about species-specific interactions between protozoa and metazoa (Verity & Smetacek 1996). Such knowledge is required if we are to identify keystone species in plankton trophodynamics, understand how the coupling of the microbial and classical food chains affects vertical flux, and how changes in the physical environment drive plankton dynamics and, thereby, the regulation of vertical carbon flux (Verity & Smetacek 1996, Wassmann 1998).

Here I examine the distribution and abundance of the dominant phytoplankton, protozoa and metazoa in Ellis Fjord. I show how intra-seasonal changes in the physical environment, together with the life-cycle ecologies of individual species and functional trophic groups, elicit changes in food web structure over short time-intervals.

3.2 Methods

3.2.1 Sampling

Two ice cores were taken randomly at the site on 3 December 1997 using a SIPRE ice-corer. The bottom 10 cm of the core was collected and transported back to the laboratory in an insulated container, and two equal sections were processed for separate analyses of chlorophyll *a* and protist identification. Each section was melted in 500 ml of 0.2 μm filtered seawater. A known

volume of this meltwater was filtered through a Whatman® 25 mm GF/F filter for analysis of chlorophyll *a* concentration, and pigments extracted as per Parsons et al. (1984). Absorbance of the extracts was measured using a GBC® UV-Vis 916 spectrophotometer at 664, 647, and 630 nm wavelengths, and the chlorophyll *a* concentration calculated (Jeffrey & Humphrey 1975). Five hundred ml of sample was preserved in acidified Lugol's iodine and sedimented in Utermöhl chambers to allow identification of protists using an inverted microscope. Due to time and logistical constraints, no further ice cores were collected.

Water column samples were taken at approximately weekly intervals from early December 1997 to mid March 1998. A 2 L Kemmerer bottle was deployed through a 20 cm hole drilled through the ice to obtain water samples at 5, 10, 20 and 40 m. Three replicate samples were taken from each depth. Each sample was transferred to a 2 L polycarbonate jar, placed in a dark, insulated container, and transported to the laboratory at Davis station. A known volume of sample was analysed, as above, for chlorophyll *a* concentration, and the mean and standard error calculated. Five hundred ml of the sample was preserved with approximately 0.4% v/v final concentration acidified Lugol's iodine to allow identification and enumeration of protists. While this fixative, like other fixatives (e.g. formalin, formaldehyde, and glutaradlehyde), can result in the loss of protist cells it is reportedly preferable to other fixatives for the fixation of ciliates (Ohman & Snyder 1991, Sherr & Sherr 1993, Leakey et al. 1994). Protists were settled in Utermöhl sedimenting chambers and examined using an inverted microscope (see Chapter 2, 2.2.3.2). Some protists, such as nanoflagellates may therefore have been under-estimated due to losses by fixation and settling. Protists were identified and counted only from samples taken on 4, 11, 18 & 25 January and 1, 8 & 18 February, as the chlorophyll *a* concentration in the water column indicated peak production during these months. Two of the three independent replicate samples were analysed for each sampling date due to the time involved in such detailed analyses. Fifteen replicate fields (or portions thereof) were counted per sample, as this was shown to reduce the variance between fields and provide a reliable estimate of the mean, and the mean and standard error calculated. Dinoflagellates were grouped as autotrophic or heterotrophic according to

Tomas (1996). I did not attempt to determine their feeding mode throughout the study. Therefore, the mixotrophic species *Amphidinium* spp. and *Ceratium* spp. were included in both the auto- and heterotrophic groups. This resulted in an over-estimation of the total abundance of auto-and heterotrophic dinoflagellates. However, the difference in total abundance with and without these species was relatively small, and generally within the range of the standard error.

Mesozooplankton were collected with an umbrella net, with a mouth of 28 x 28 cm and a mesh size of 100 μm (Kirkwood & Burton, 1987). This mesh size was chosen to ensure the best possible sampling efficiency for the majority of small metazoa, except nauplii (Pasternak et al. 2000). A larger mesh size severely under-estimates the abundance of small metazoa, while a smaller sized mesh would have led to clogging by the phytoplankton bloom (Beaumont & Hosie 1997, Gallienne & Robins 2001). The net was deployed through 20 cm holes drilled through the ice cover. Three holes were drilled at random in the sea ice. The samples were taken from four depths, 5, 10, 20 and 40 m to surface at each hole, thereby providing three replicate samples for each depth. The samples were preserved in 5% Steedman's solution containing 5 % buffered formalin, 4.5% propylene glycol, and 0.5% propylene phenoxytol (Steedman 1976). In the laboratory, all the copepods, an abundant ctenophore, and echinopluteus larvae were identified and counted. These taxa accounted for > 90% of the total metazoan abundance. Mesozooplankton abundance was calculated using the mouth area of the net and the vertical distance towed, assuming 100% filtration efficiency. These values were subtracted from consecutive depths to determine abundance at the following depth intervals: 0 - 5, 5 - 10, 10 - 20, and 20 - 40 m.

3.2.2 Multivariate statistical analysis

Details of the multivariate analysis techniques, as modified from Field et al. (1982) and Kruskal & Wish (1978), have been described previously in Hosie (1994a,b), Hosie & Cochran (1994), Beaumont & Hosie (1997) and Hosie et al. (1997). Multivariate analyses were carried out using BIOΣTAT III (Pimental, R.A. and Smith, J.D., Sigma Soft, Placentia, California). The methodology used in the present study is described below and summarised in a flow diagram (Figure 3.1).

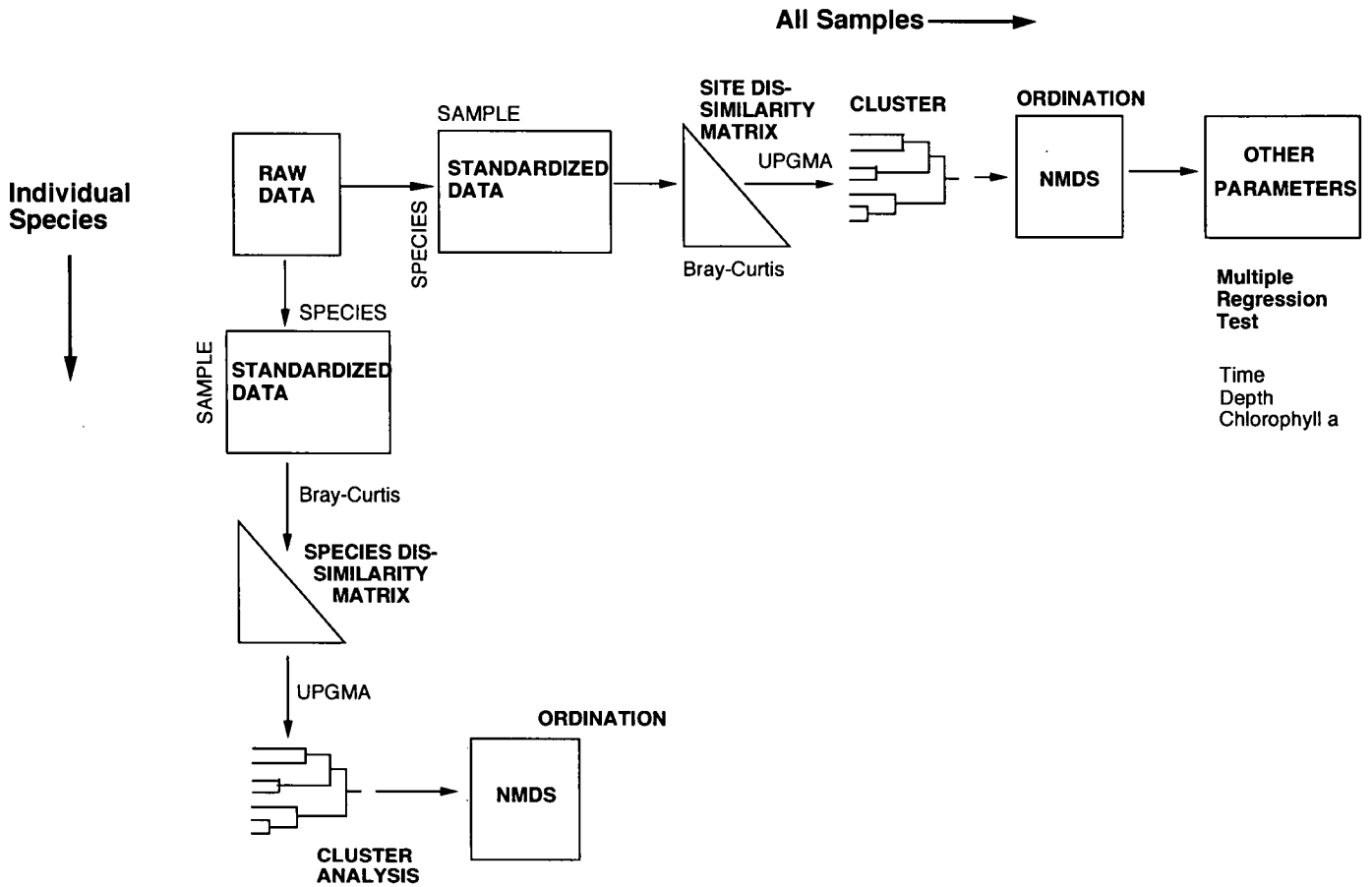


Figure 3.1. Diagrammatic summary of the steps used in the multivariate analyses to define species relationships, sample associations, and influence of time, depth and chlorophyll*a* concentration on species and sample groups. UPGMA = unweighted pairs group mean average linkage, NMDS = non-metric multidimensional scaling. Adapted from Hosie (1994).

Prior to analysis, species data were standardised as in Field et al. (1982) i.e. :

$$Y_{ij} = 100X_{ij} / \sum_{j=1}^{n} X_{ij} \qquad \text{(Equation 3.1)}$$

where X_{ij} = abundance of the *i* th species in the *j* th sample;

$\sum_{j=1}^{n} X_{ij}$ = summed abundance of the *i* th species over all samples;

Y_{ij} = corresponding standardised score.

3.2.2.1 Cluster analysis

Analysis of all samples, time, and depth, by all species, combined in one matrix was made by cluster analysis. Cluster analysis is a way of grouping sites based on the degree of dissimilarity of species composition. The Bray-Curtis dissimilarity index was used to produce a dissimilarity matrix (Bray and Curtis 1957). This index is commonly used in the analysis of ecological data, as it is able to cope with large numbers of zero values. To provide a visual ouput, the groupings are displayed in the form of a dendrogram. This dendrogram was produced with the unweighted pairs group average linkage (UPGMA) sorting strategy. The dendrogram shows the dissimilarity between cluster groups based on the average inter-group value. Therefore cluster analysis determined sample associations based on the dissimilarity of species in time and space. A transposed cluster analysis, i.e. a species by sample matrix, identified species associations. Furthermore, analyses of all dates for individual depths, and all depths for individual dates were performed. These analyses were examined in light of the prior determination of species associations. All cluster analyses were verified by subsequent ordination.

3.2.2.2 Ordination

Ordination is a procedure for adapting a multidimensional swarm of data points in two dimensions to reveal any intrinsic pattern in the data (Kruskal and Wish 1978). A number of ordination techniques exist, such as Principal Component Analysis, Reciprocal Averaging, Detrended Correspondence Analysis, and Non-metric Multi-dimensional Scaling (NMDS). I chose to analyse my data by NMDS as it is considered to be the most robust ordination technique (Gray et al. 1988). It is able to cope with non

homogeneous data, and provides a stress value indicating the degree of fit between the original and derived data sets (Field et al. 1982, Gray et al. 1988). NMDS is an interative process that regresses the distances between the ecological data points on the corresponding dissimilarities thereby providing ordination scores (two dimensional coordinates) for each of the data points (Field et al. 1982). The output is a two dimensional map based on the ranked measure of dissimilarity between samples.

3.2.2.3 Multiple regression

New ordination scores derived from NMDS are independent scores summarising all the ecological data and can be used to investigate any relationship between the data and other parameters. I examined the relationship between all samples and the parameters time, depth and chlorophyll *a* concentration. Multiple regression of each parameter (dependent variable) on the ordination scores (independent variables) identifies the parameters that correlate significantly with the data, and the adjusted r^2 values provide the percentage variation the parameters explain in the data (Jongman et al. 1987). The direction of the regression line (at maximum correlation) is at an angle q_r with the r th axis. Therefore the direction of the regression line in space is described by the cosines of this angle. These are termed the direction cosines, or regressions weights, c_r and are derived from Kruskal and Wish's (1978) formula:

$$c_r = b_r / \sqrt{b_1^2+b_2^2+...b_m^2} \qquad \text{(Equation 3.2)}$$

where b_1, b_2, are the regression coefficients from the multiple regression $a+b_1x_1+b_2x_2+...b_mx_m$, where m is the number of independent variables x_i.

3.3 Results

3.3.1 Chlorophyll a

Chlorophyll *a* concentrations recorded from two ice cores were 36.16 μg L^{-1} and 4.76 μg L^{-1} on 3 December 1997. These cores were dominated by *Pinnularia quadratarea* v. *constricta, Pseudonitzschia* spp., and *Polarella glacialis. Pleurosigma* spp. and dinoflagellate cysts were also present.

Chlorophyll *a* concentration in the water column was low throughout December and early January (Figure 3.2). A preliminary peak was observed in mid-January at 5 and 20 m. The major peak in chlorophyll *a* concentration occurred on 18 February at all depths. While the highest concentration of 27.57 $\mu g\ L^{-1}$ was recorded at 10 m, overall chlorophyll *a* concentration showed minimal variation between depths.

3.3.2 Phytoplankton

Diatoms generally dominated the protistan assemblage in the water column, exhibiting two major peaks during the season. The first peak occurred at 5 m in early January, with a mean concentration of 1.50×10^6 cells L^{-1} (Figure 3.3). *Fragilariopsis curta, Pseudonitzschia subcurvata,* and *Thalassiosira ambigua* were the major contributing species. Other diatoms present were *Fragilariopsis cylindrus, Chaetoceros* spp., *Pinnularia* spp., *Entomoneis kjellmanii, Coscinodiscus* spp., and *Pleurosigma* spp. The second peak occurred at 10 m on 18 February with a mean concentration of 2.31×10^6 cells L^{-1}. This resulted from a sudden bloom of nanoplanktonic diatoms, predominantly *Fragilariopsis pseudonana. Thalassiosira ambigua* was also present, while *Pinnularia* spp. and *Coscinodiscus* spp. reached their peak concentrations on this date (Table 3.1). Overall, diatom concentration was highest in the upper 10 m of the water column, while the concentration was much lower at depths of 20 and 40 m.

Autotrophic flagellates increased in concentration at lower depths before peaking at 5 m on 25 January with a mean concentration of 6.44×10^6 cells L^{-1} (Figure 3.4). The concentration declined rapidly thereafter. This peak concentration consisted almost entirely of the cryptophyte *Geminigera cryophyllum,* with occasional occurrence by the silicoflagellate *Dictyocha speculum.*

Autotrophic dinoflagellates were in low concentration throughout January at all depths in the water column (Figure 3.5). The concentration increased in February and peaked at 10 m (1.85×10^5 cells L^{-1}) on 18 February. The dominant species were *Gymnodinium* spp., *Polarella glacialis* and *Ceratium* spp., with *Gymnodinium* spp. dominating in the upper water column. *Prorocentrum* spp. were also present.

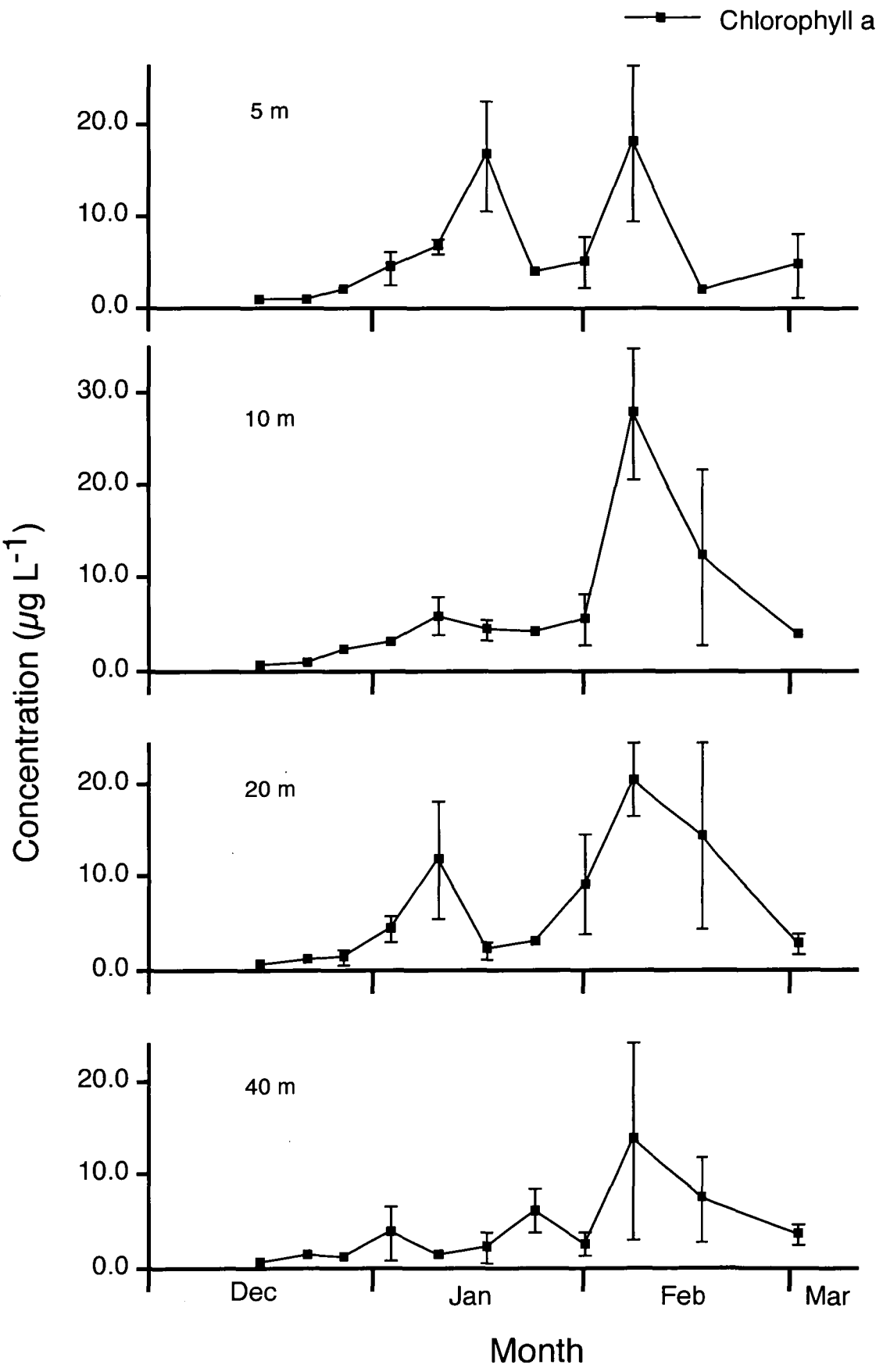


Figure 3.2. Chlorophyll *a* concentration at 5, 10, 20, and 40 m in the water column during summer. Error bars represent ± 1 SE.

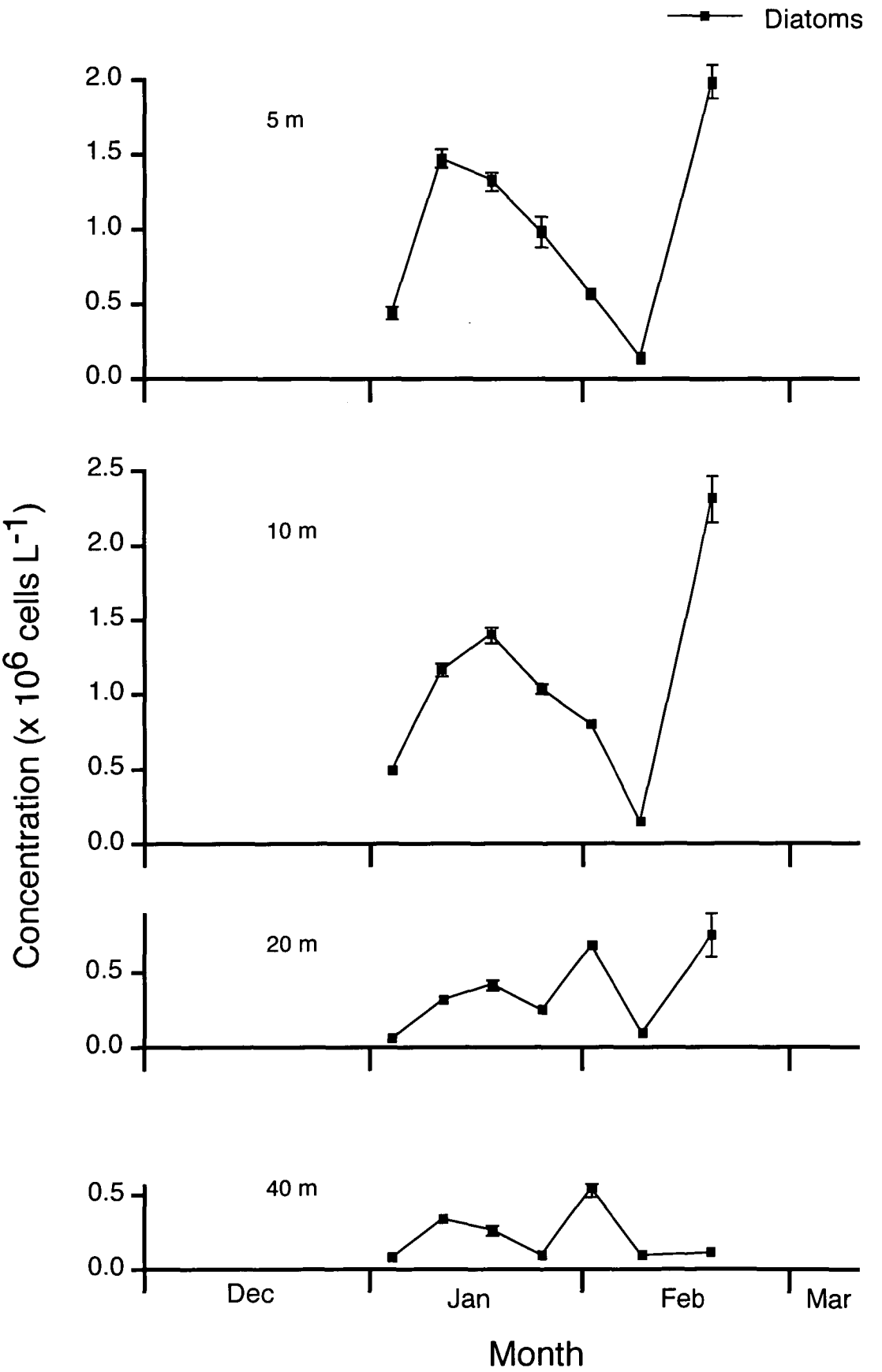


Figure 3.3. Diatom concentration at 5, 10, 20, and 40 m in the water column during summer. Error bars represent ± 1 SE.

Table 3.1. Mean (± SE) concentration of ice-associated diatoms (x 10^3 cells L^{-1}) at depth intervals from surface to 40 m in Ellis Fjord. – signifies absent from the water column.

Species	Date	5 m	10 m	20 m	40 m
Pinnularia quadratarea v. *constricta*	4 Jan	0.23 (0.23)	-	0.06 (0.04)	-
	11 Jan	-	0.46 (0.46)	-	-
	18 Jan	0.23 (0.23)	-	-	-
	25 Jan	-	-	-	-
	1 Feb	-	-	-	-
	8 Feb	-	0.46 (0.46)	-	-
	18 Feb	3.49 (1.20)	2.10 (0.83)	-	-
Entomoneis kjellmanii	4 Jan	-	0.69 (0.69)	0.22 (0.01)	-
	11 Jan	-	-	-	-
	18 Jan	-	-	-	-
	25 Jan	-	0.46 (0.46)	-	-
	1 Feb	-	-	-	-
	8 Feb	-	-	0.93 (0.93)	-
	18 Feb	-	-	0.08 (0.08)	-
Coscinodiscus spp.	4 Jan	-	-	0.06 (0.06)	0.12 (0.06)
	11 Jan	-	-	-	-
	18 Jan	-	-	-	-
	25 Jan	-	-	0.12 (0.12)	0.12 (0.12)
	1 Feb	-	-	-	-
	8 Feb	-	-	-	-
	18 Feb	-	4.19 (1.52)	-	-

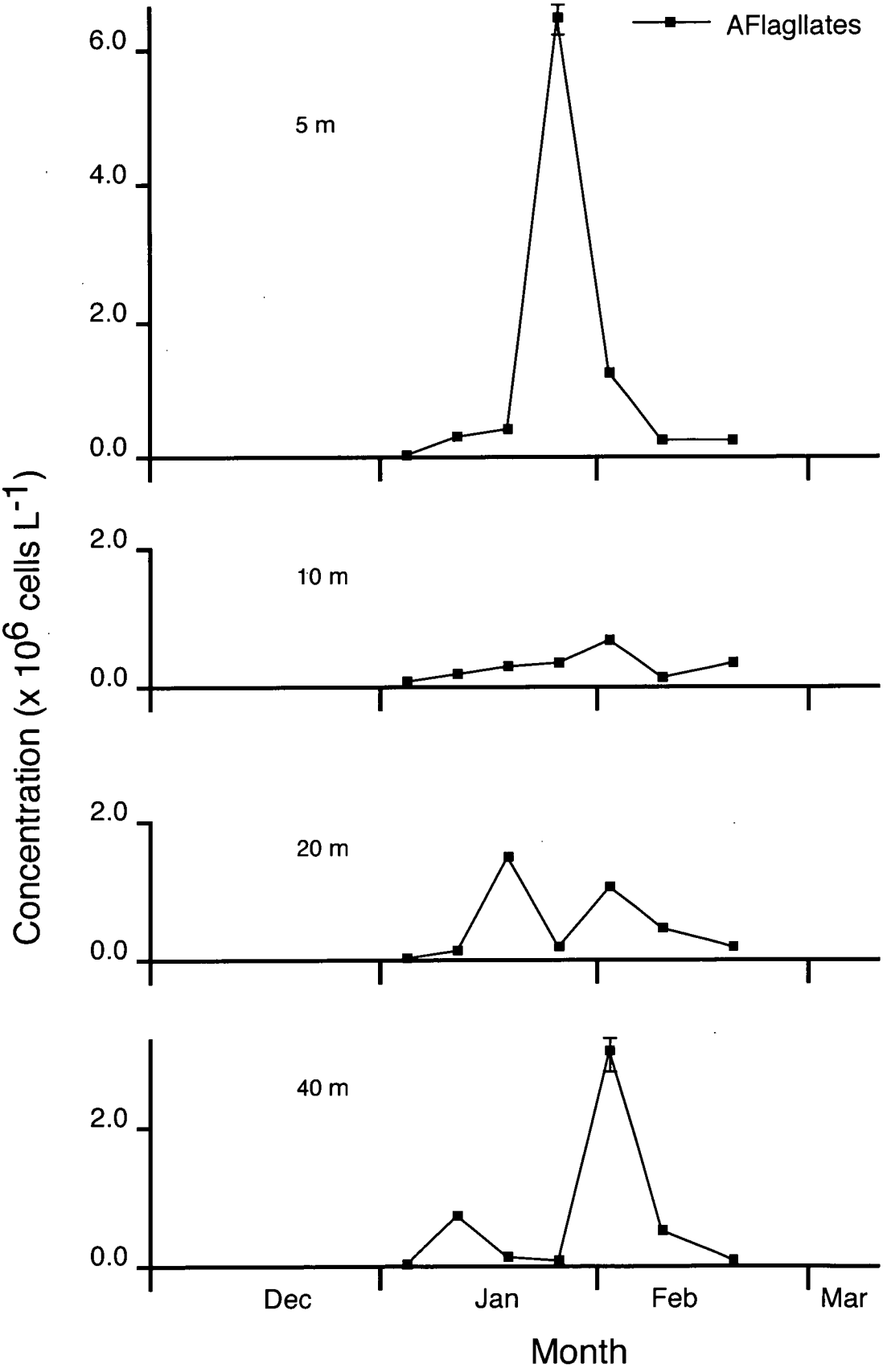


Figure 3.4. Concentration of autotrophic flagellates (AFlagellates) at 5, 10, 20, and 40 m in the water column during summer. Error bars represent ± 1 SE.

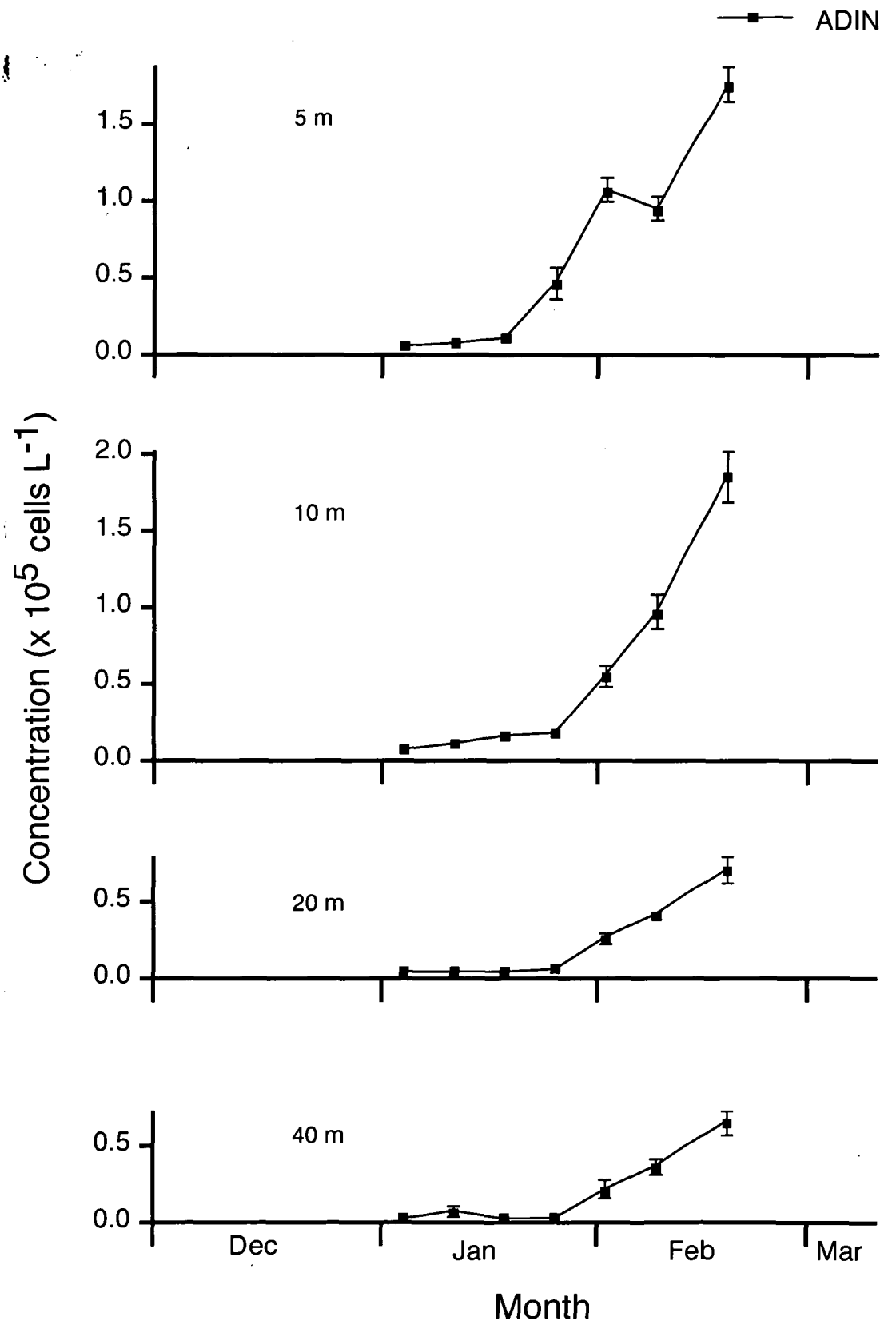


Figure 3.5. Autotrophic dinoflagellate (ADIN) concentration at 5, 10, 20, and 40 m in the water column during summer. Error bars represent ± 1 SE.

Dinoflagellate cysts were most abundant in the upper 10 m of the water column (Figure 3.6). Concentrations were low throughout most of January but increased towards the end of the month and reached a peak concentration of 12.60 x 10^4 cells L^{-1} on 18 February.

3.3.3 Protozoa

All heterotrophic species showed a similar temporal pattern of abundance to the autotrophic dinoflagellates, with low concentrations throughout January, increasing to a peak in February. Heterotrophic dinoflagellates in the water column peaked at a concentration of 6.33 x 10^4 cells L^{-1} at 5 m on 1 February and thereafter declined (Figure 3.7). The peak at 10 m occurred one week later. At the lower depths (20 and 40 m), the concentration steadily increased over the month to peak on 18 February. The mixotrophic *Ceratium* spp. were the numerically dominant species, however *Gyrodinium* spp. and *Katodinium* spp., at times, contributed substantially to the biomass. *Amphidinium* spp. and *Protoperidinium* spp. were also present.

Heterotrophic nanoflagellates in the water column peaked in February (Figure 3.8). This occurred at all depths except 10 m, where the peak occurred in mid-January. The nanoflagellates were generally spherical and measured approximately 6 μm in diameter. It is possible that some crysophyte statocysts were included as nanoflagellates.

Ciliates were in low concentration at all depths throughout the season. The exception was a peak at 5 m on 8 February, with a continued high concentration one week later (Figure 3.9). The ciliates were not identified to species, however two morphological types, one resembling *Strombidium* spp., as well as tintinnids were recorded.

3.3.4 Metazoa

Small copepods generally dominated the mesozooplankton. *Oncaea curvata* was the dominant copepod, with a peak of 631 m^{-3} from surface to 20 m depth in early January (Figure 3.10). The abundance of this species was greatest during January, and thereafter declined in February and March. *Paralabidocera antarctica* and *Oithona similis* were the next most abundant species, although they occurred in much lower abundance than *O. curvata*,

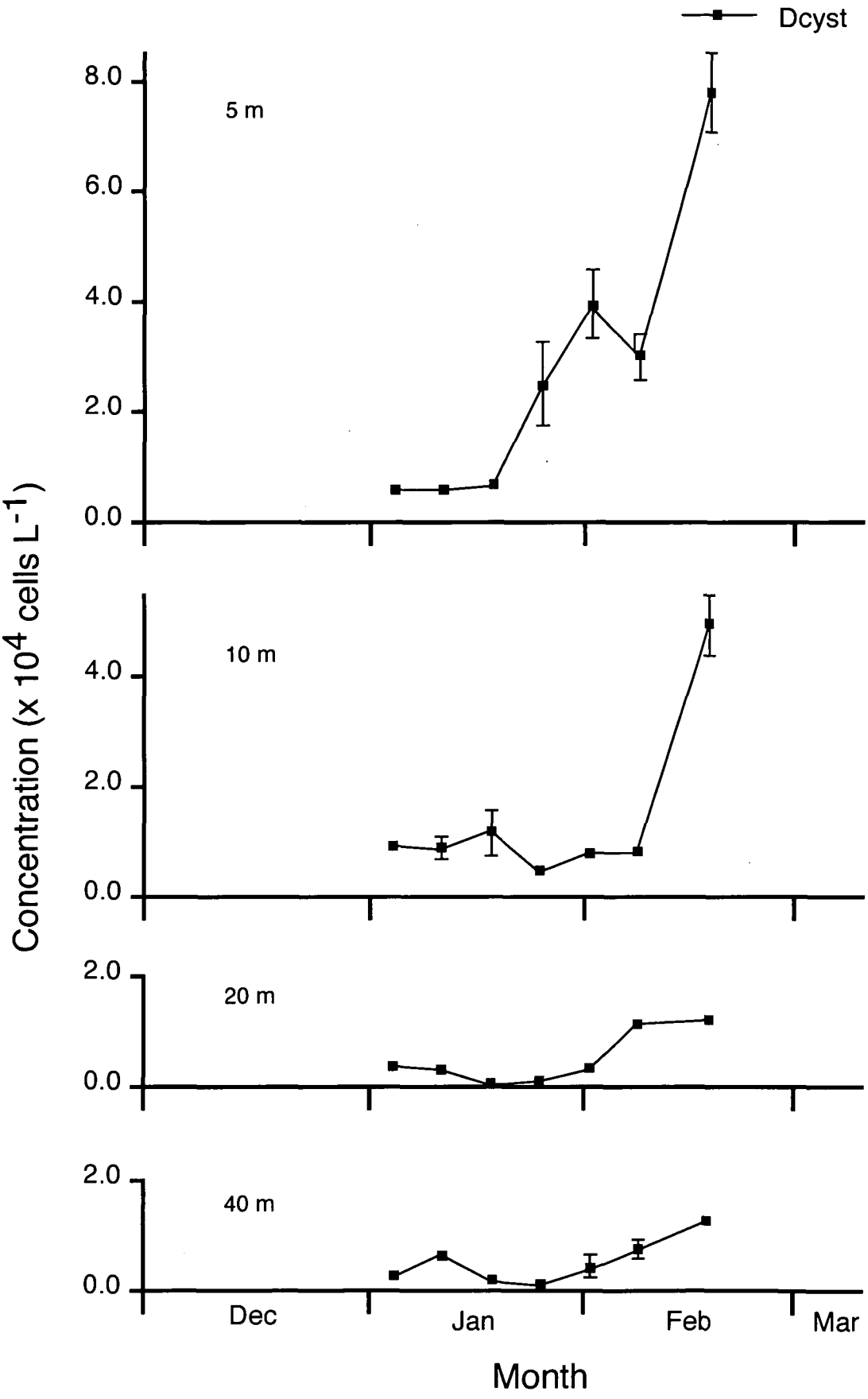


Figure 3.6. Dinoflagellate cyst (Dcyst) concentration at 5, 10, 20, and 40 m in the water column during summer. Error bars represent ± 1 SE.

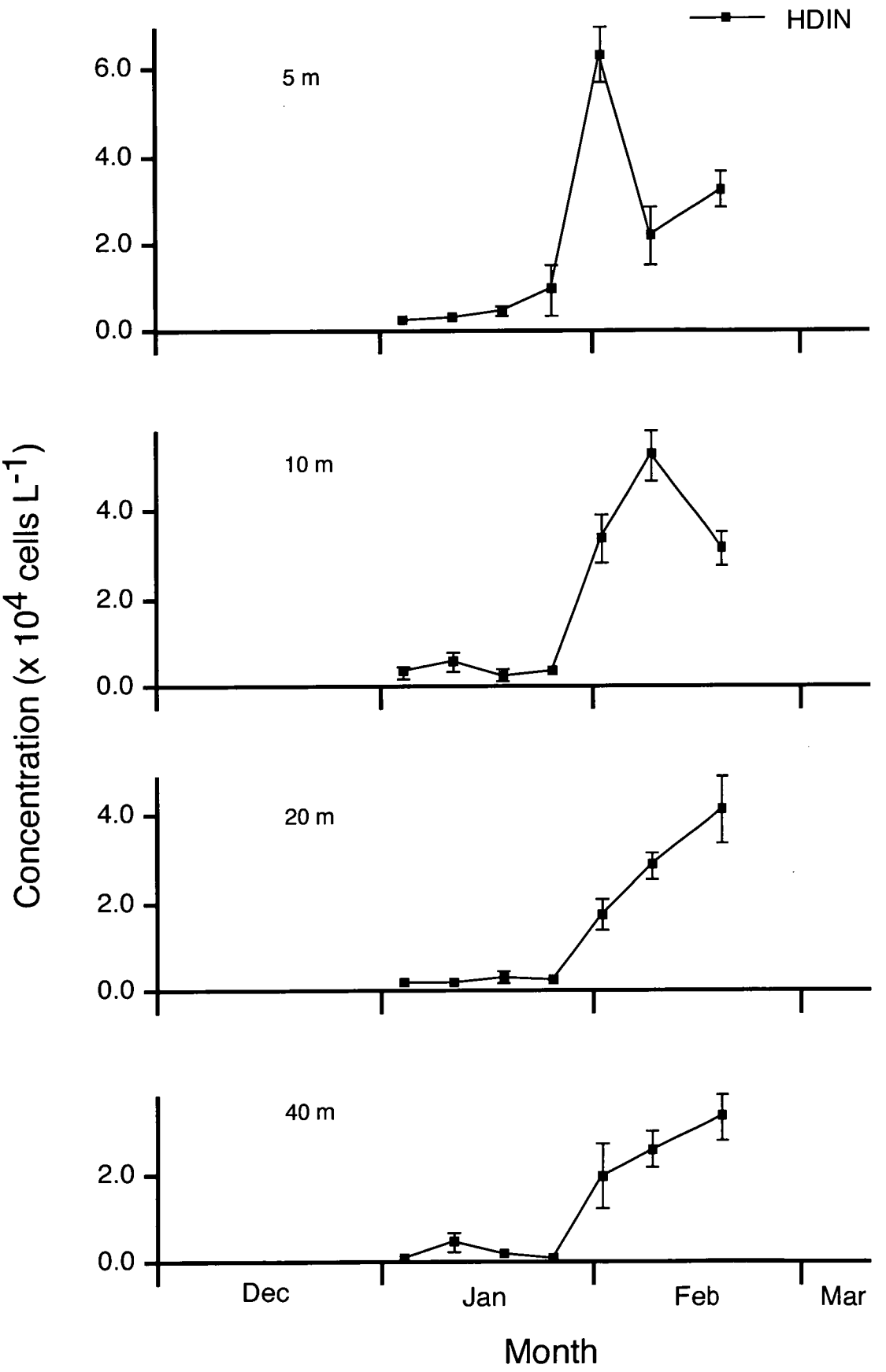


Figure 3.7. Heterotrophic dinoflagellate (HDIN) concentration at 5, 10, 20, and 40 m in the water column during summer. Error bars represent ± 1 SE.

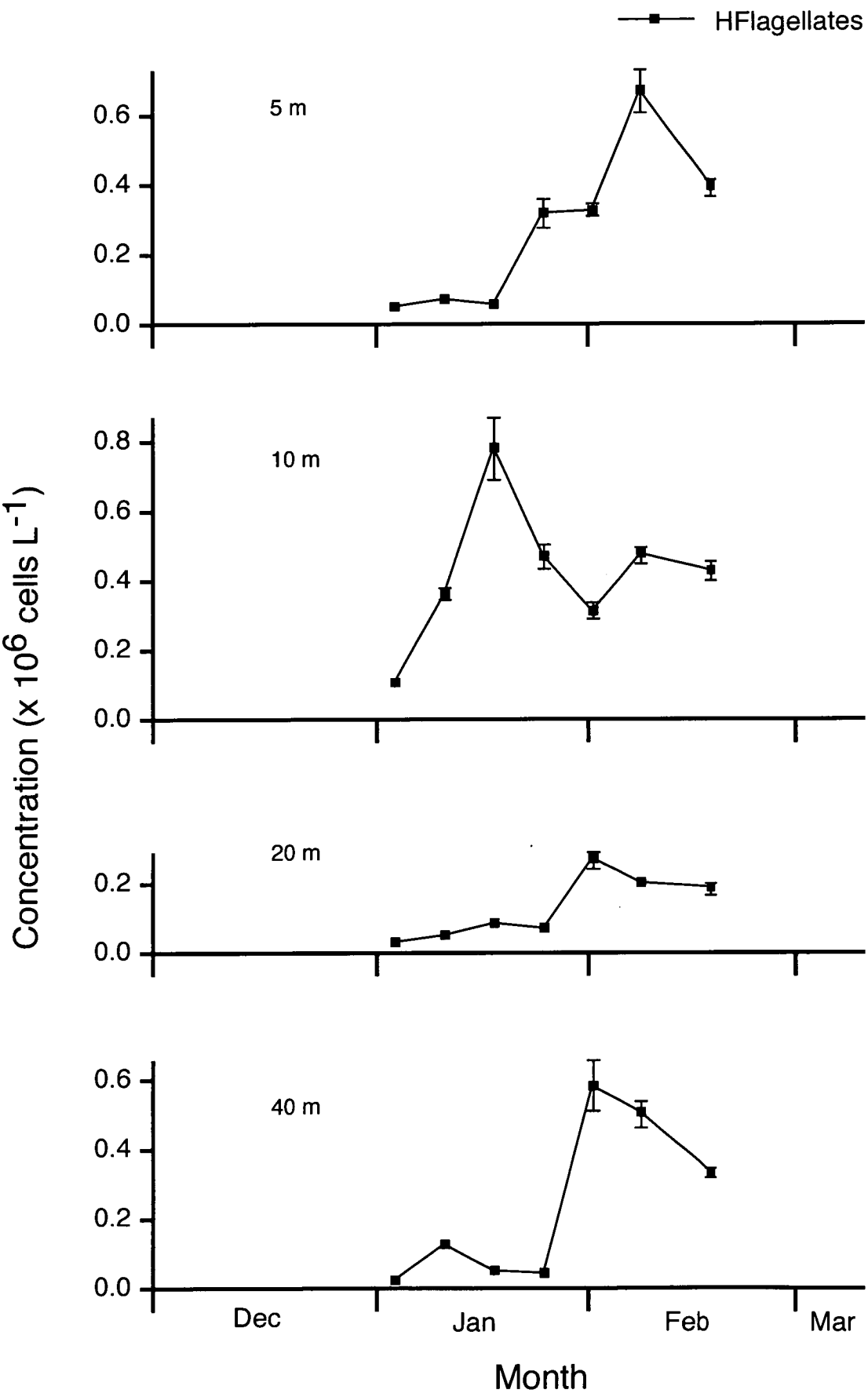


Figure 3.8. Heterotrophic nanoflagellate (HFlagellate) concentration at 5, 10, 20, and 40 m in the water column during summer. Error bars represent ± 1 SE.

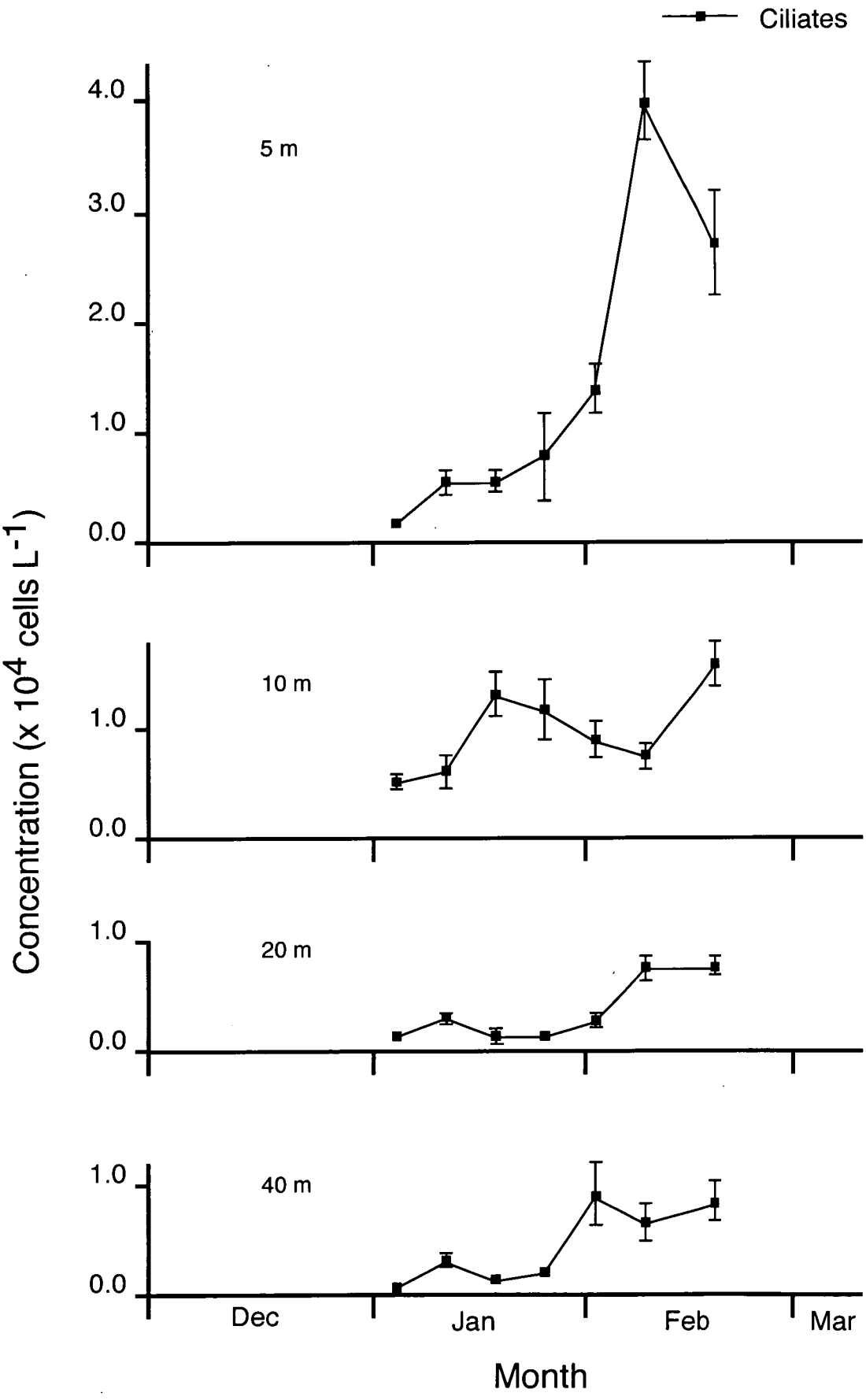


Figure 3.9. Ciliate concentration at 5, 10, 20, and 40 m in the water column during summer. Error bars represent ± 1 SE.

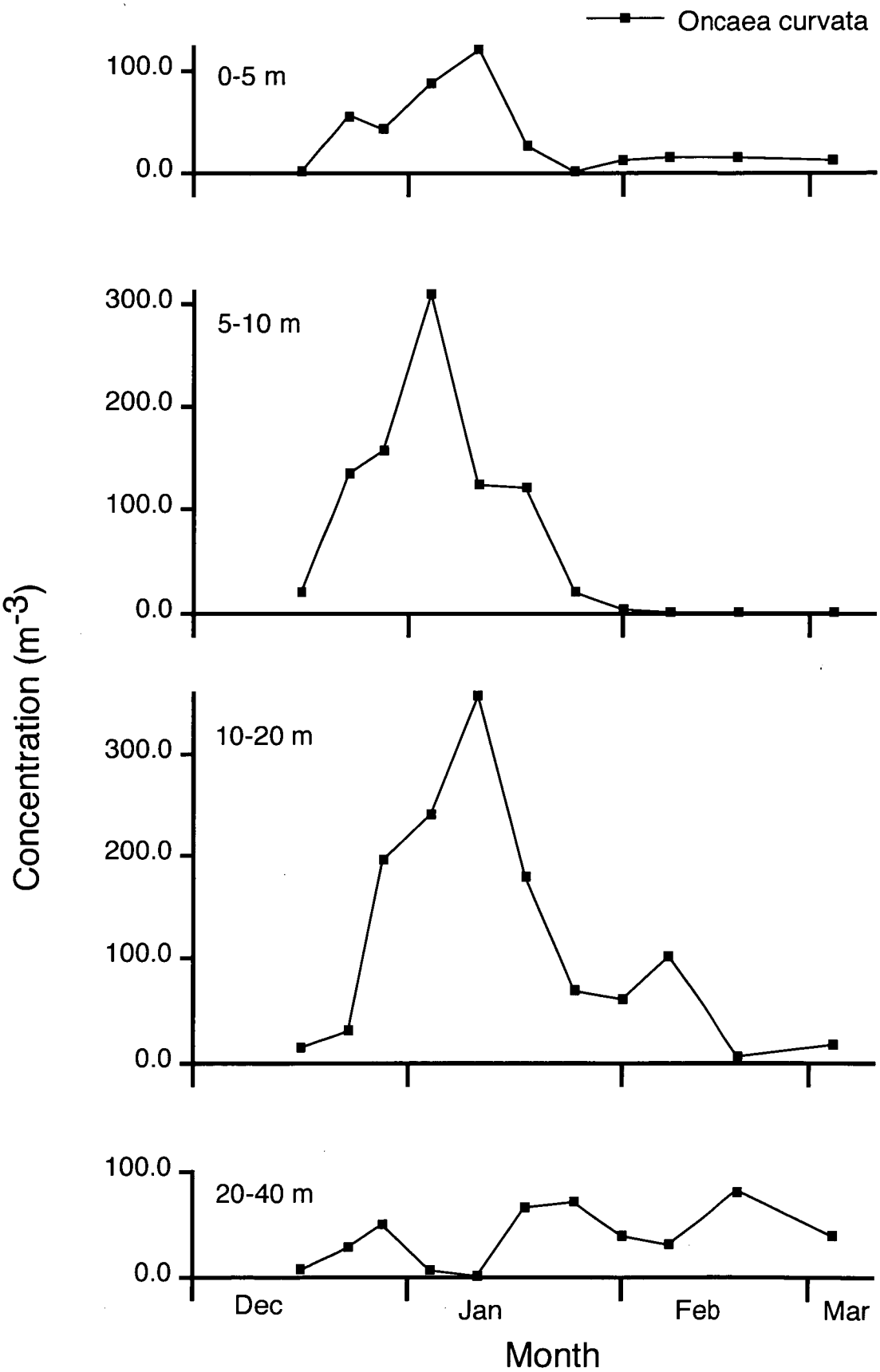


Figure 3.10. The integrated abundance of *Oncaea curvata* from 0-5 m, 5-10 m, 10-20 m, and 20-40 m in the water column.

averaging < 30 m^{-3} (Figures 3.11 & 3.12). *Paralabidocera antarctica* was found predominantly in the upper 5 m of the water column, was in highest abundance from mid-December to mid-January, but declined in February and was absent in March. In contrast, *O. similis* peaked in mid February and early March between 0 and 20 m in the water column. *Ctenocalanus citer* was present in low abundance from January to March (Figure 3.13), while harpacticoid copepods exhibited a short-lived peak of 19 ind m^{-3} on 18 January (Figure 3.14).

The large copepods were in much lower abundance than the small copepods. *Calanoides acutus* was the dominant large copepod, with a peak of 32 m^{-3} (Figure 3.15). *Calanoides acutus* occurred in the water column from the surface to 20 m depth and was only abundant from February to March. *Drepanopus bispinosus* was in lower abundance and was only present between mid February and early March (Figure 3.16). *Stephos longipes* and *Euchaeta antarctica* were occasionally present in very low abundance throughout the entire season.

Two taxa exhibited short-lived blooms in the upper 5 m of the water column, the lacustrine *Daphniopsis studeri* from 25 January to 8 February (Figure 3.17), and echinopluteus larvae on 1 February (Figure 3.18). Echinopluteus larvae showed the greatest single numerical peak of the mesozooplankton at 939 ind m^{-3}.

An unidentified cydippid ctenophore, most likely *Callianira cristata*, occurred in waters from surface to 20 m depth (Figure 3.19). The peak abundance of 170 m^{-3} occurred in the upper 10 m of the water column in early January.

3.3.5 Multivariate analysis of ecological interactions

The cluster analysis of all samples (time, depth and species) defined three groups at 71% dissimilarity (Figure 3.20a). Group A was the upper 10 m of the water column from 4-18 January, and 20 m on 18 January, Group B was generally the lower 20 & 40 m of the water column throughout January, while the upper 10 m of the water column on 25 January and almost all depths during February comprised Group C. The three outliers observed were all from 40 m, on 4 & 25 January and 8 February. Groups A & B

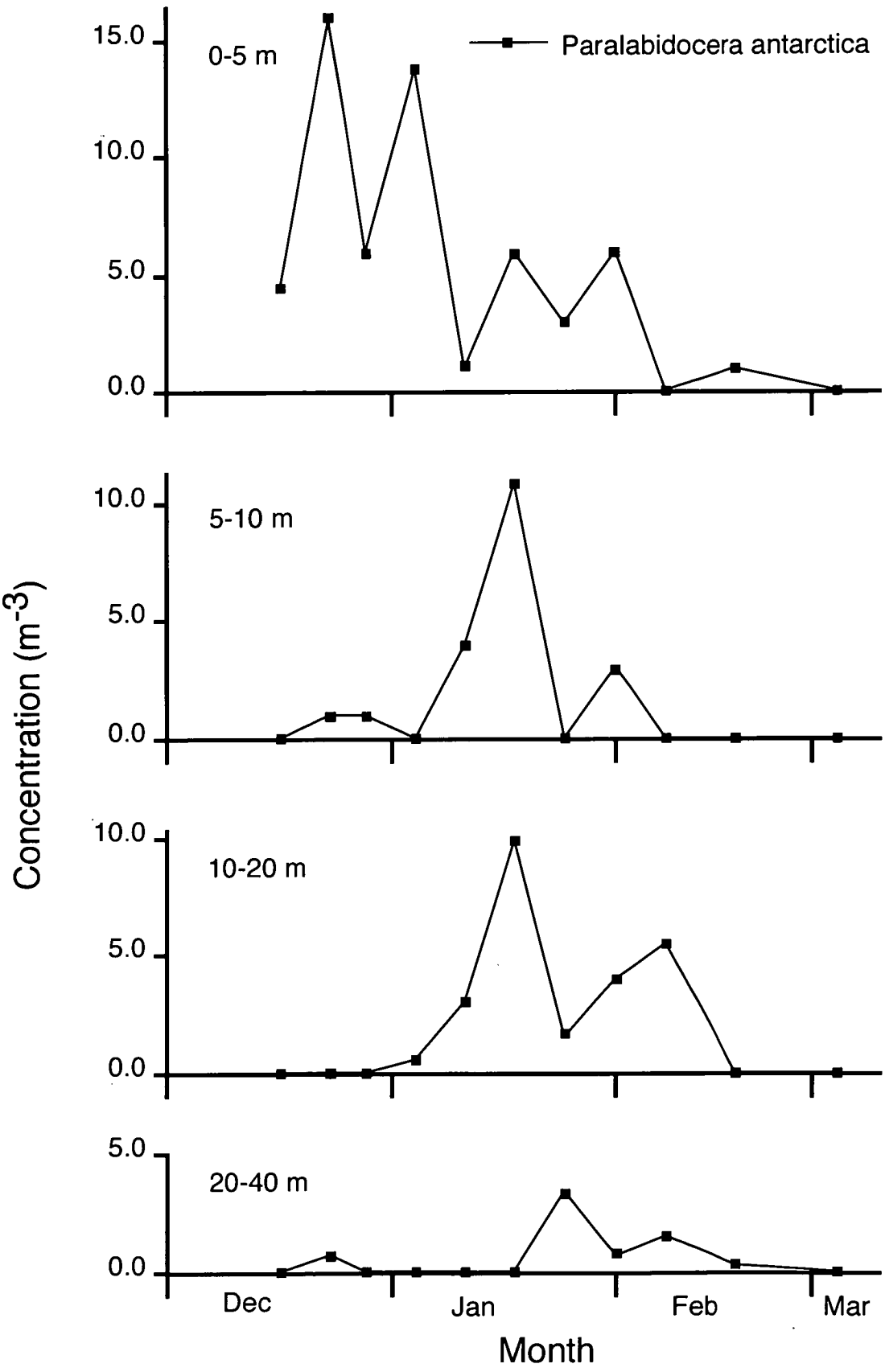


Figure 3.11. The abundance of *Paralabidocera antarctica* at 0-5 m, 5-10 m, 10-20 m, and 20-40 m in the water column.

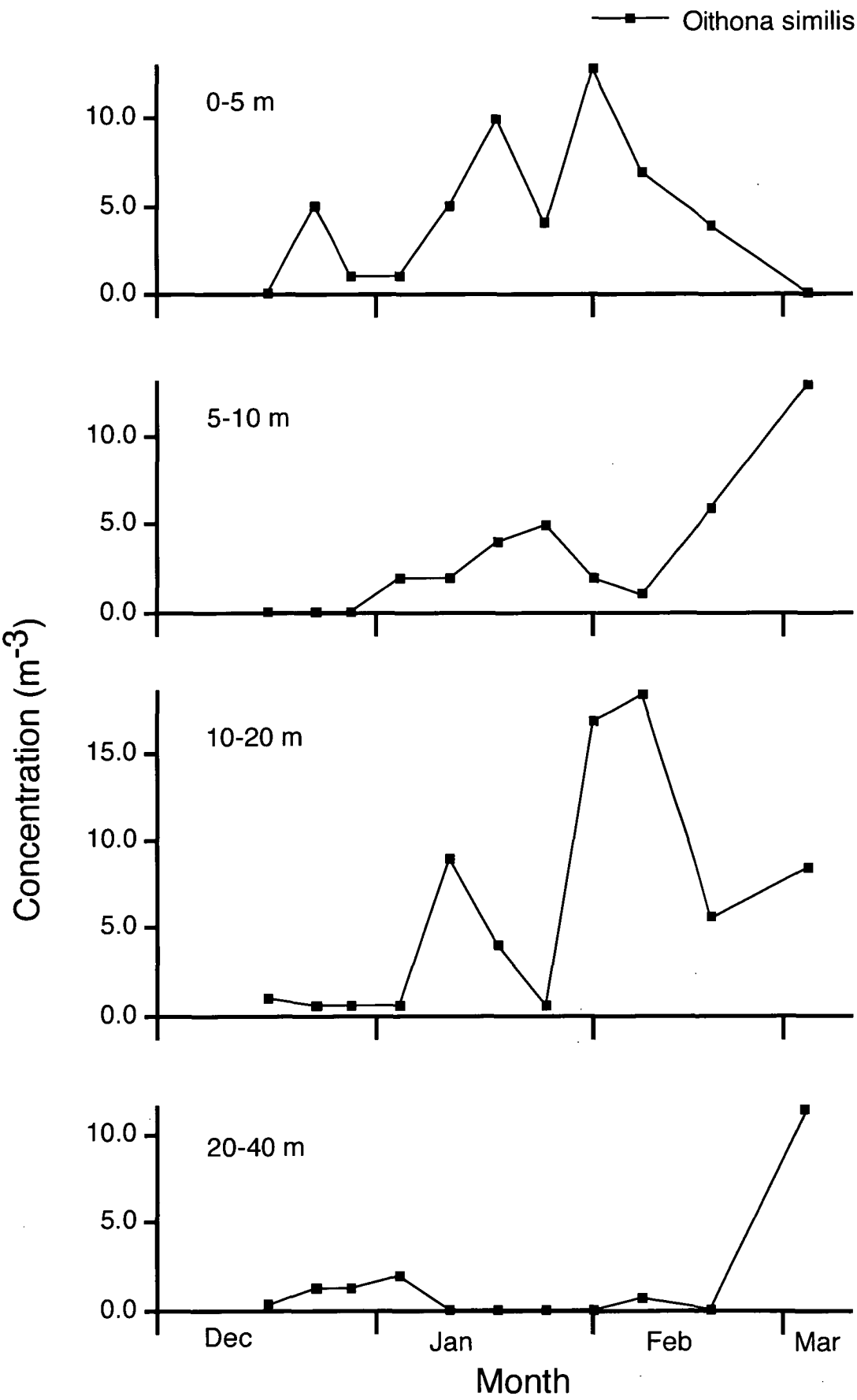


Figure 3.12. The integrated abundance of *Oithona similis* from 0-5 m, 5-10 m, 10-20 m, and 20-40 m in the water column.

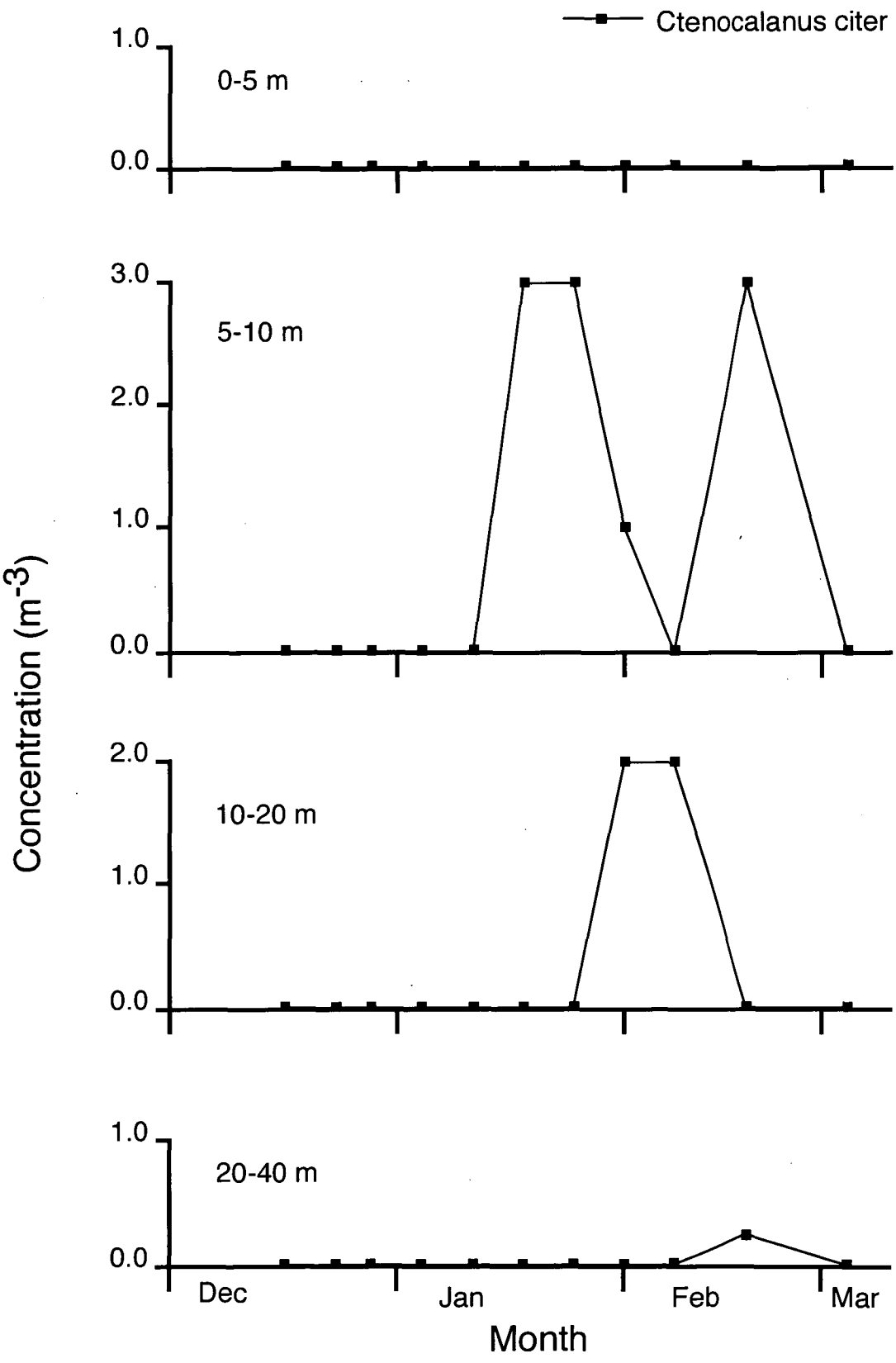


Figure 3.13. The integrated abundance of *Ctenocalanus citer* from 0-5 m, 5-10 m, 10-20 m, and 20-40 m in the water column.

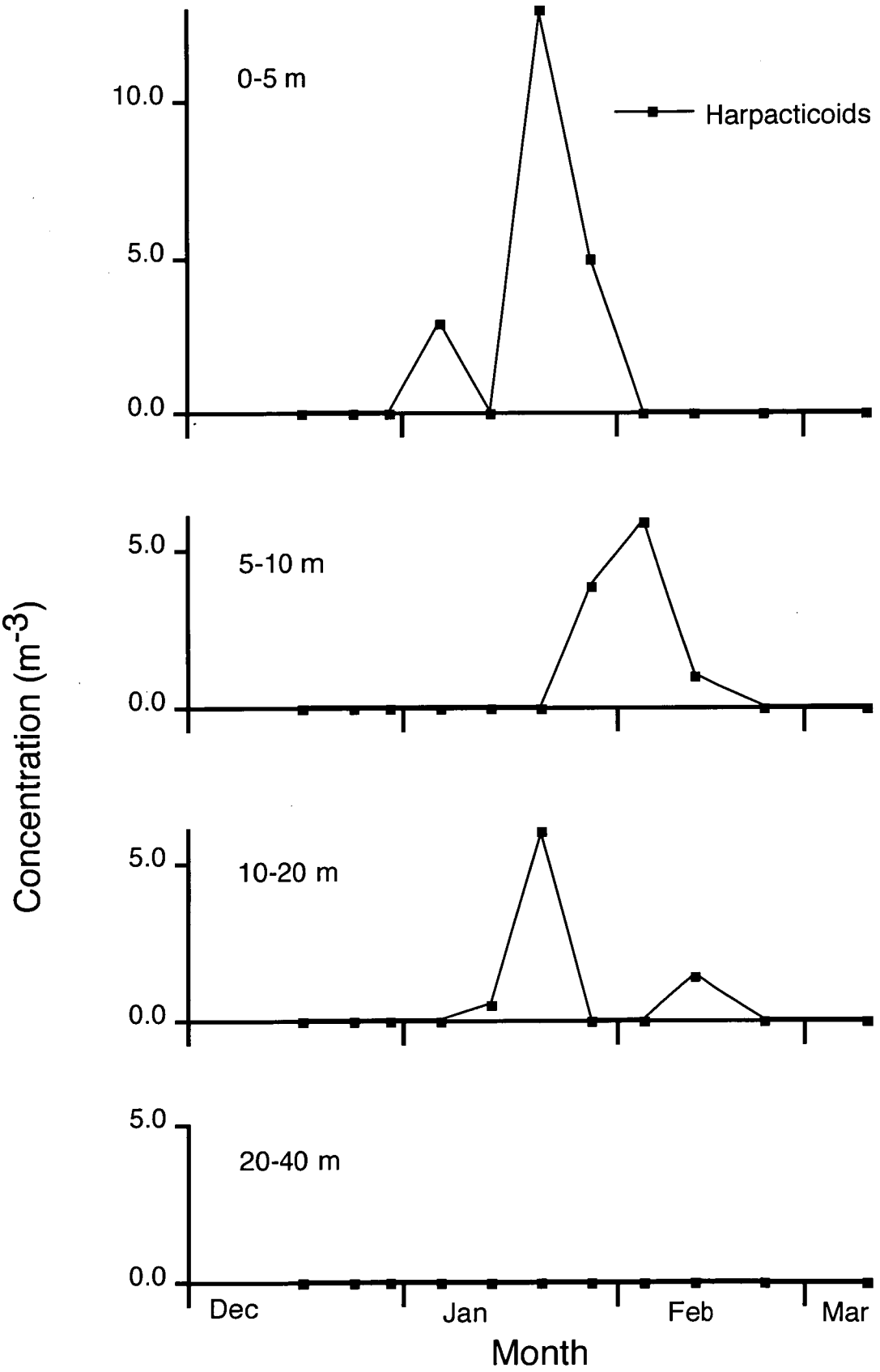


Figure 3.14. The integrated abundance of harpacticoid copepods from 0-5 m, 5-10 m, 10-20 m, and 20-40 m in the water column.

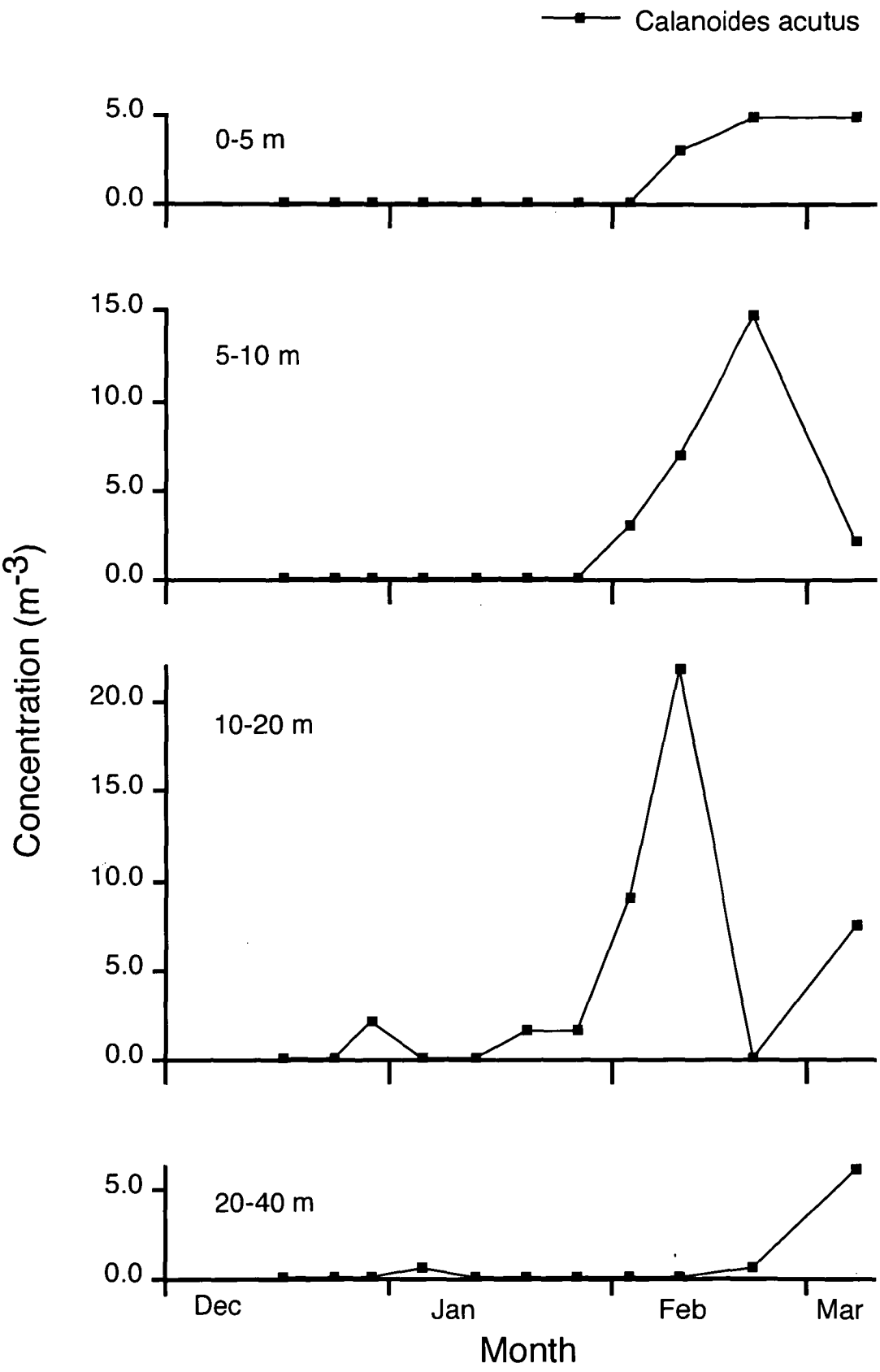


Figure 3.15. The integrated abundance of *Calanoides acutus* from 0-5 m, 5-10 m, 10-20 m, and 20-40 m in the water column.

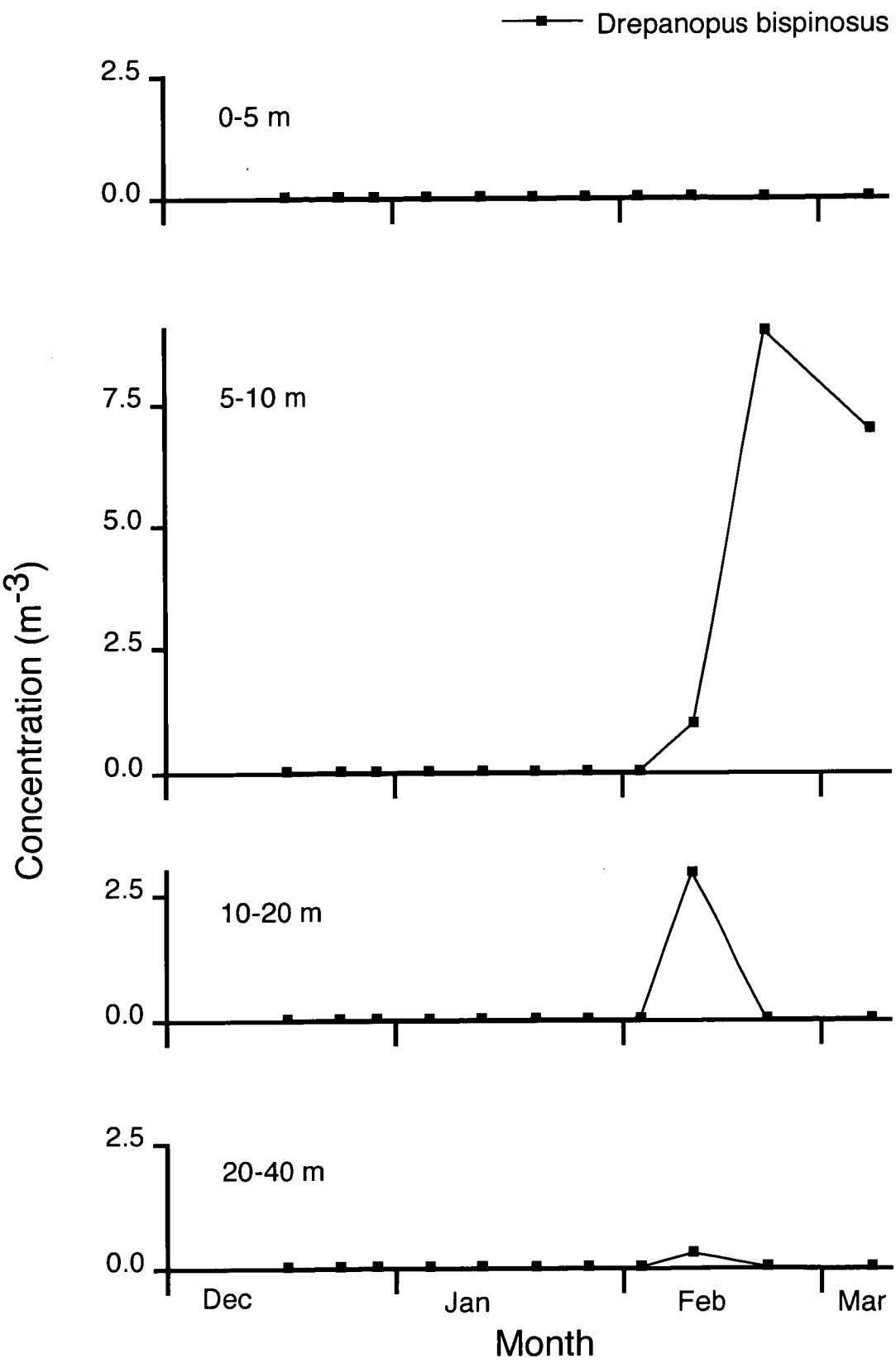


Figure 3.16. The integrated abundance of *Drepanopus bispinosus* from 0-5 m, 5-10 m, 10-20 m, and 20-40 m in the water column.

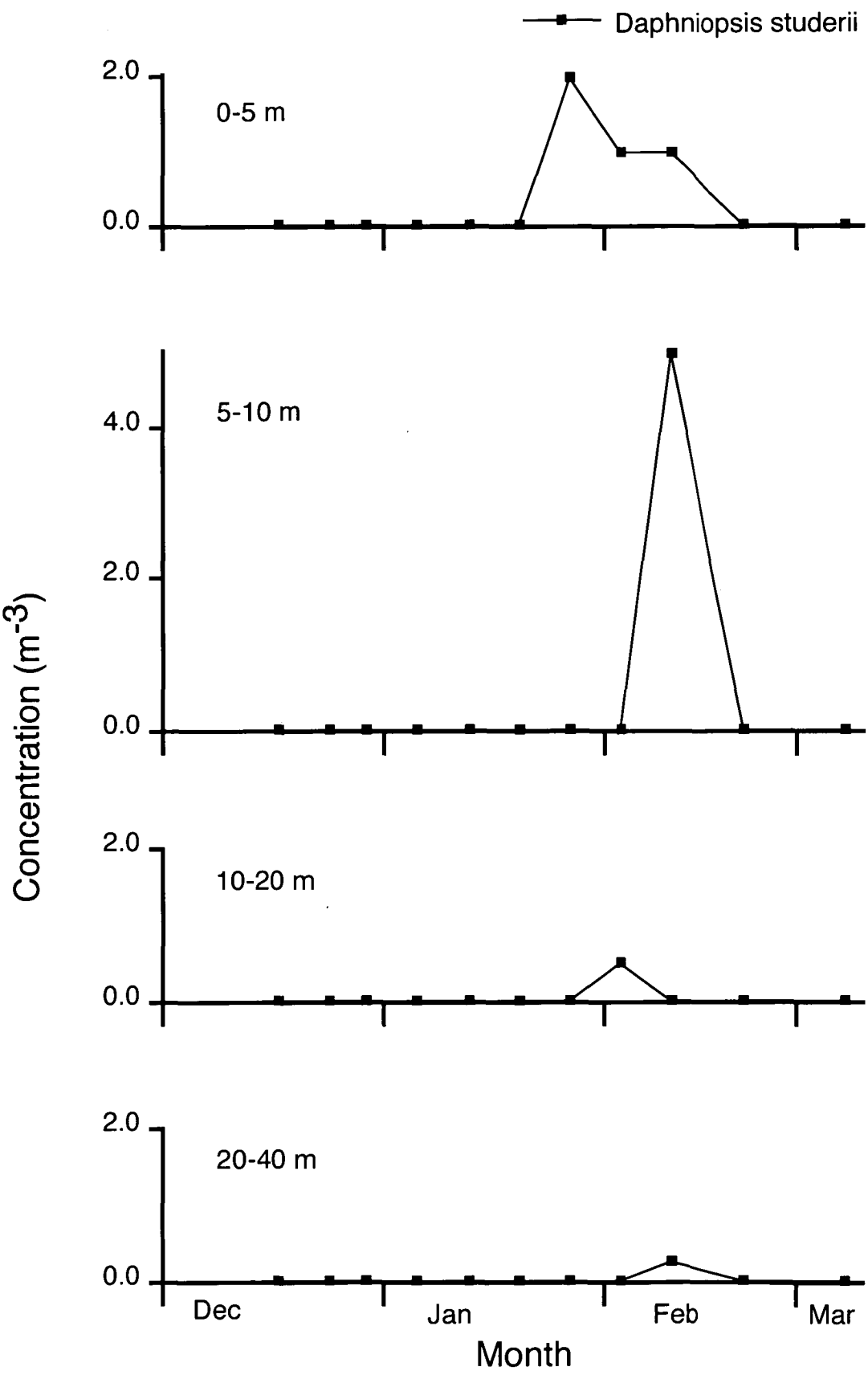


Figure 3.17. The integrated abundance of *Daphniopsis studerii* from 0-5 m, 5-10 m, 10-20 m, and 20-40 m in the water column.

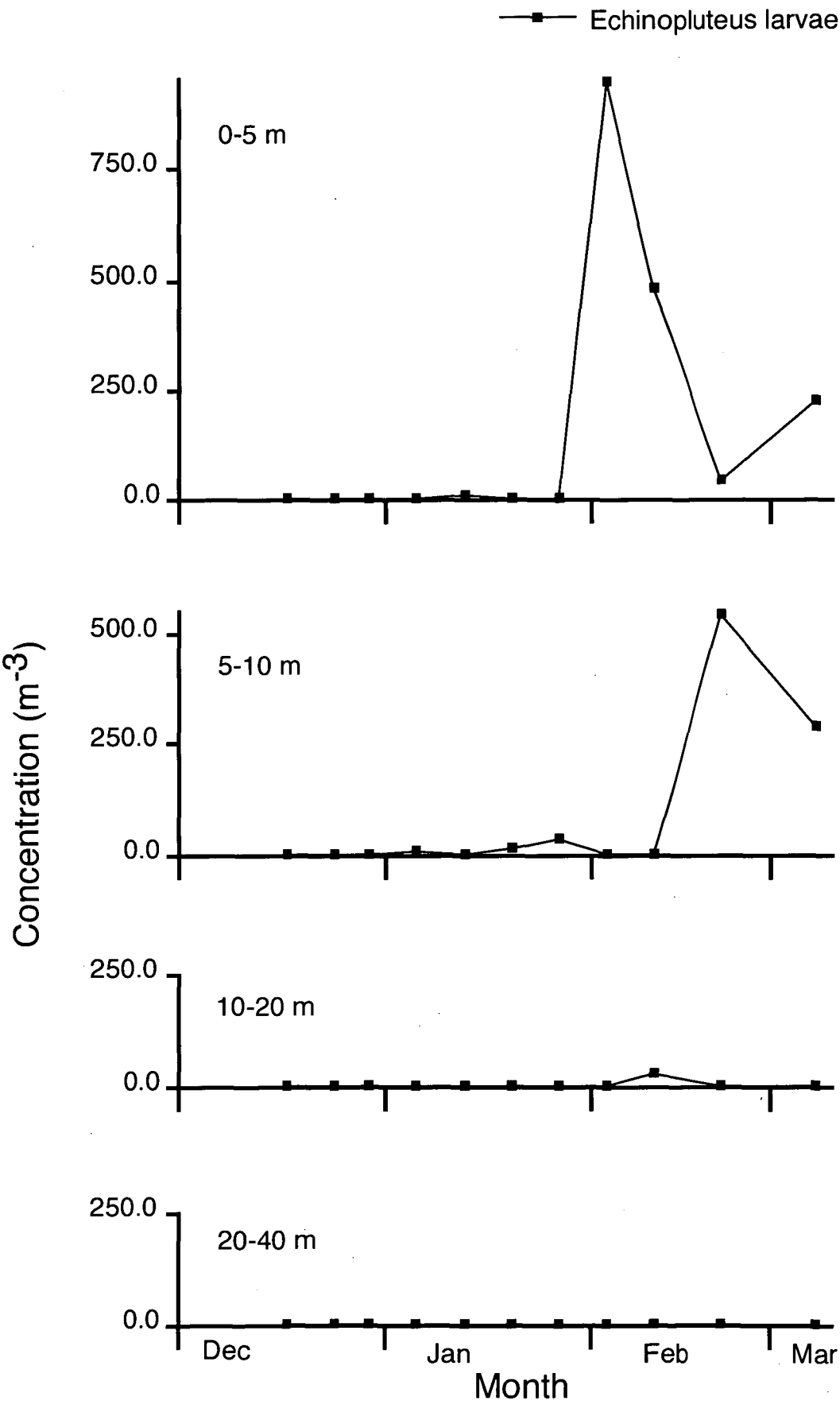


Figure 3.18. The integrated abundance of Echinopluteus larvae from 0-5 m, 5-10 m, 10-20 m, and 20-40 m in the water column.

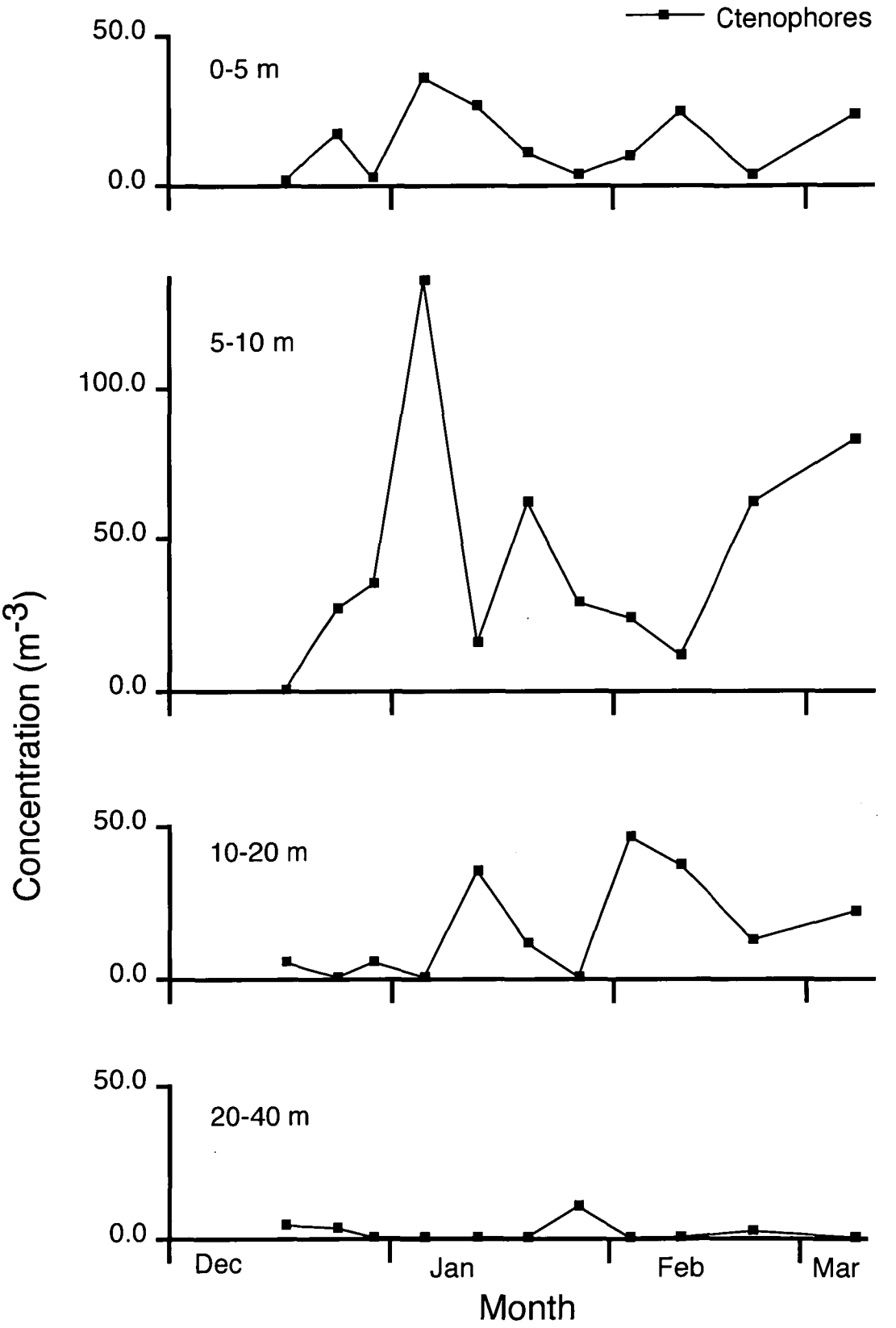


Figure 3.19. The integrated abundance of Ctenophores from 0-5 m, 5-10 m, 10-20 m, and 20-40 m in the water column.

converged at 77% dissimilarity. The ordination plots broadly confirmed these groups, and multiple regressions showed that the convergence of Groups A & B was related to time, the parameter that explained 69% of the variation in the data (Figure 3.20b). Depth explained 48% of the variance and chlorophyll *a* concentration 40%. The direction of maximum correlation for chlorophyll *a* concentration was similar to that of time.

The reverse cluster analysis defined three major species groups at 63% dissimilarity (Figure 3.21a) that, in general, were confirmed by the ordination plots (Figure 3.21b). Group 1 contained the dominant diatoms, *Fragilariopsis* spp. (1), *Chaetoceros* spp. (3), and *Nitzschia* spp. (4), the small copepods, *P. antarctica* (22), *O. curvata* (20), and the ctenophore *C. cristata* (29). Group 2 contained the centric diatom *T. ambigua* (2), *G. cryophyllum* (7), all the dinoflagellate species (9-15) except *Protoperidinium* spp. (12), dinoflagellate cysts (16), heterotrophic flagellates (17), ciliates (18), and *O. similis* (21). Nanoplanktonic diatoms, *Pinnularia* spp. (5), the larger copepods *C. acutus* (24) and *D. bispinosus* (28), and *C. citer* (26) comprised Group 3. The following species were observed as outliers: *D. studeri* (31), *D. speculum* (8), *Protoperidinium* spp. (12), *S. longipes* (25), *Euchaeta antarctica* (27), harpacticoid copepods (23) and echinopluteus larvae (30). The ordination plots showed *O. similis* closely associated with ctenophores on the border of Group 1 (Figure 3.21b).

Analyses of individual dates and depths are included in Appendix 3. The general pattern from the individual depth analyses showed that the dominant diatoms, small copepods and ctenophores were distinct from the majority of the protozoa. However, *O. similis* and ctenophores associated with the protozoan group at 10 m, and *O. similis, C. acutus, C. citer,* and *D. bispinosus* formed a separate group at 20 m depth. At 40 m, the protists (phytoplankton and protozoa) formed a single group and, with the exception of *O. curvata,* the mesozooplankton were distinctly separate from this protist group. The individual date analyses showed that in early January the mesozooplankton were separate from the protists, with the exception of *O. similis,* which was closely associated with the protozoa. In mid-January, the species groups 1 & 2 identified by reverse cluster analysis (see above) were joined, apart from a few of the dinoflagellate species that remained separate. However, by late January, these dinoflagellate species and the

a

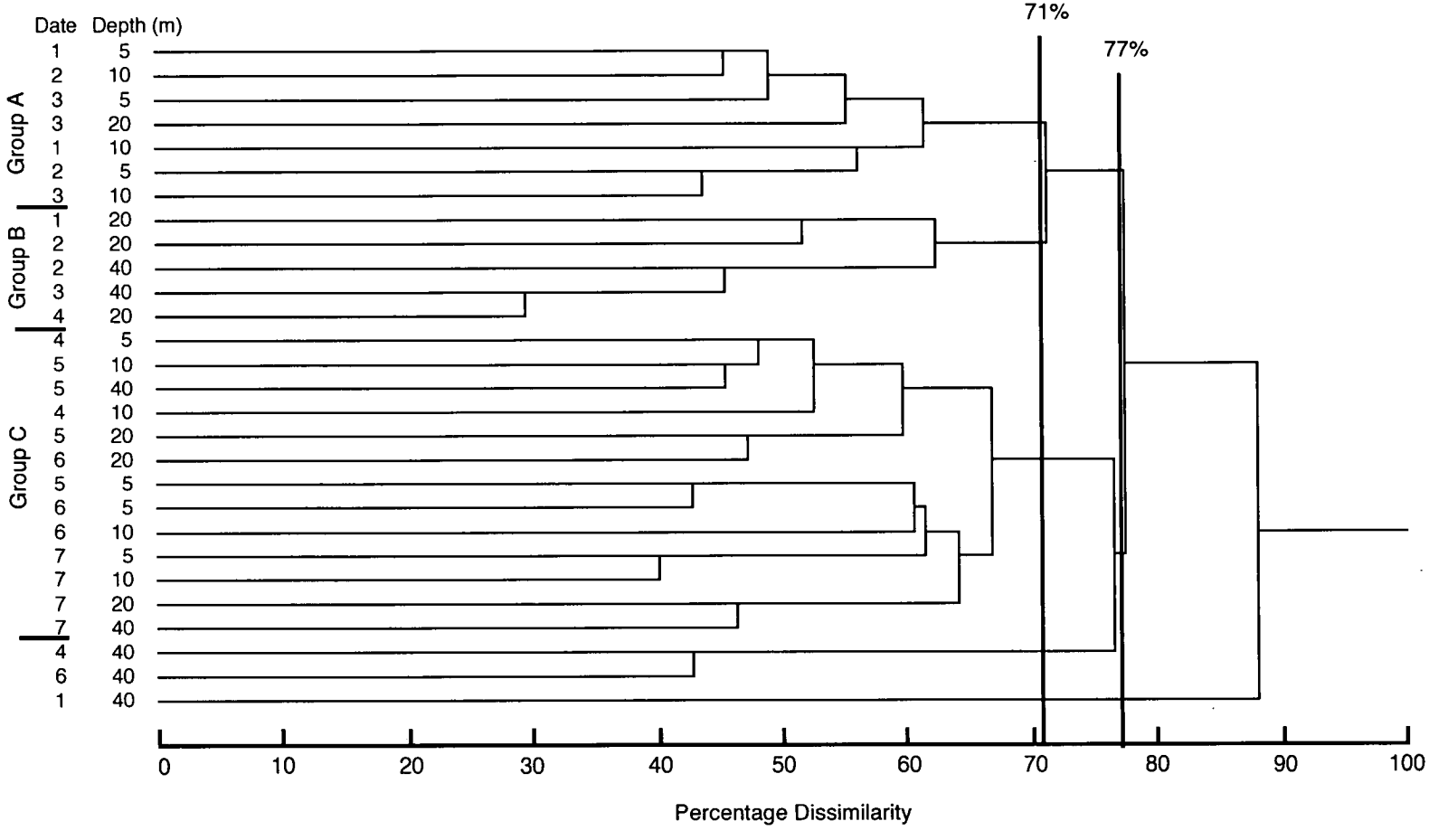


Figure 3.20a. Multivariate analysis of sample associations shows the dendrogram of cluster analysis based on the Bray-Curtis dissimilarity index with UPGMA linkage. Dates 1 - 4 represent 4, 11, 18 & 25 January, respectively, and dates 5 - 7 represent 1, 8 & 18 February, respectively.

b

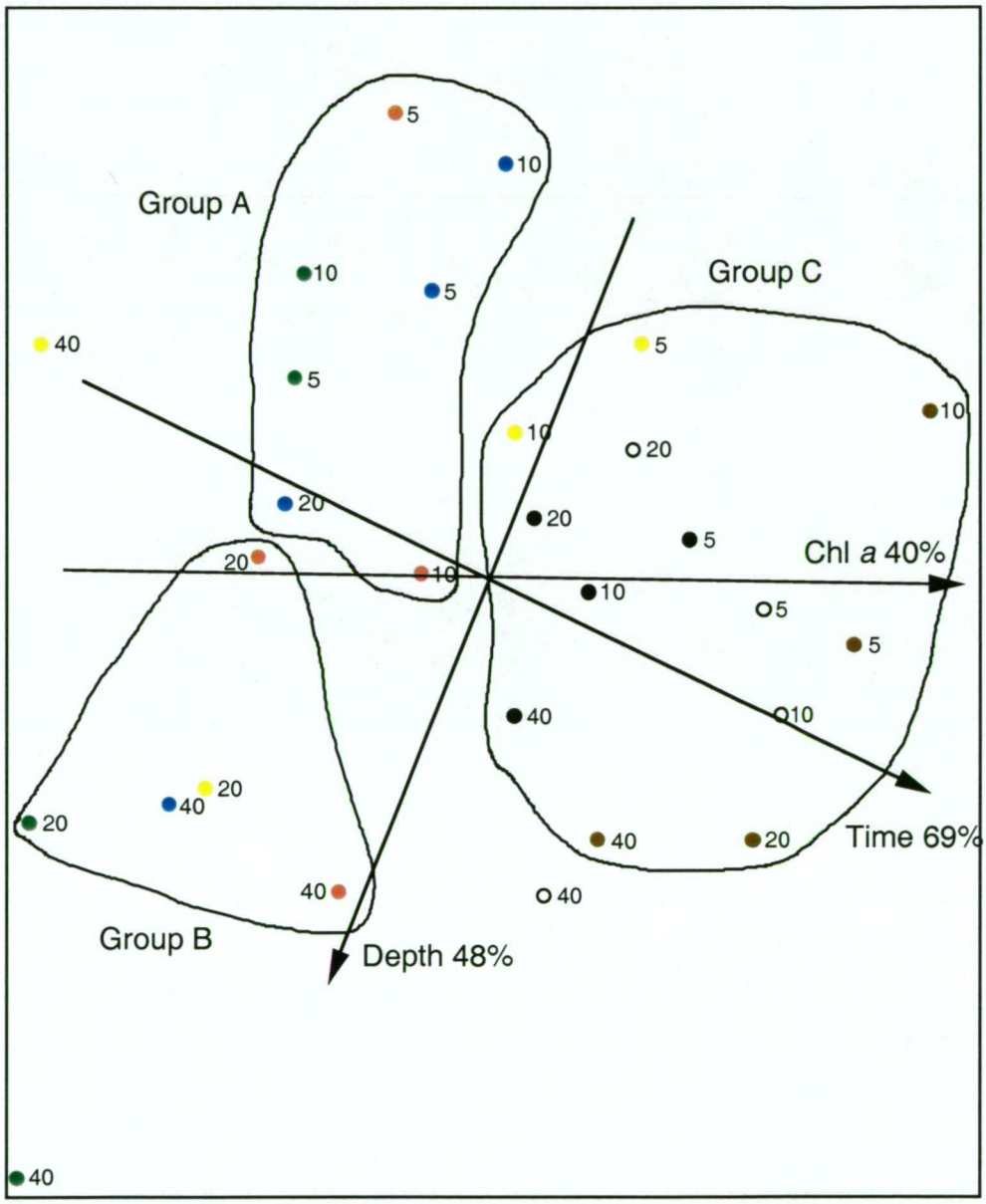


Figure 3.20b. Multivariate analysis of sample associations.shows the ordination plot of the cluster analysis using NMDS. Colours denote dates of samples. Green, red, blue & yellow represent 4, 11, 18 & 25 January, respectively. Black, white & brown represent 1, 8 &18 February, respectively. Numbers denote depth (m). Axis scales are not shown as they are relative in NMDS. Significant multiple regressions between ordination scores and time, depth, and chlorophyll *a* concentration are shown, as well as the fraction (%) of variance explained by these parameters.

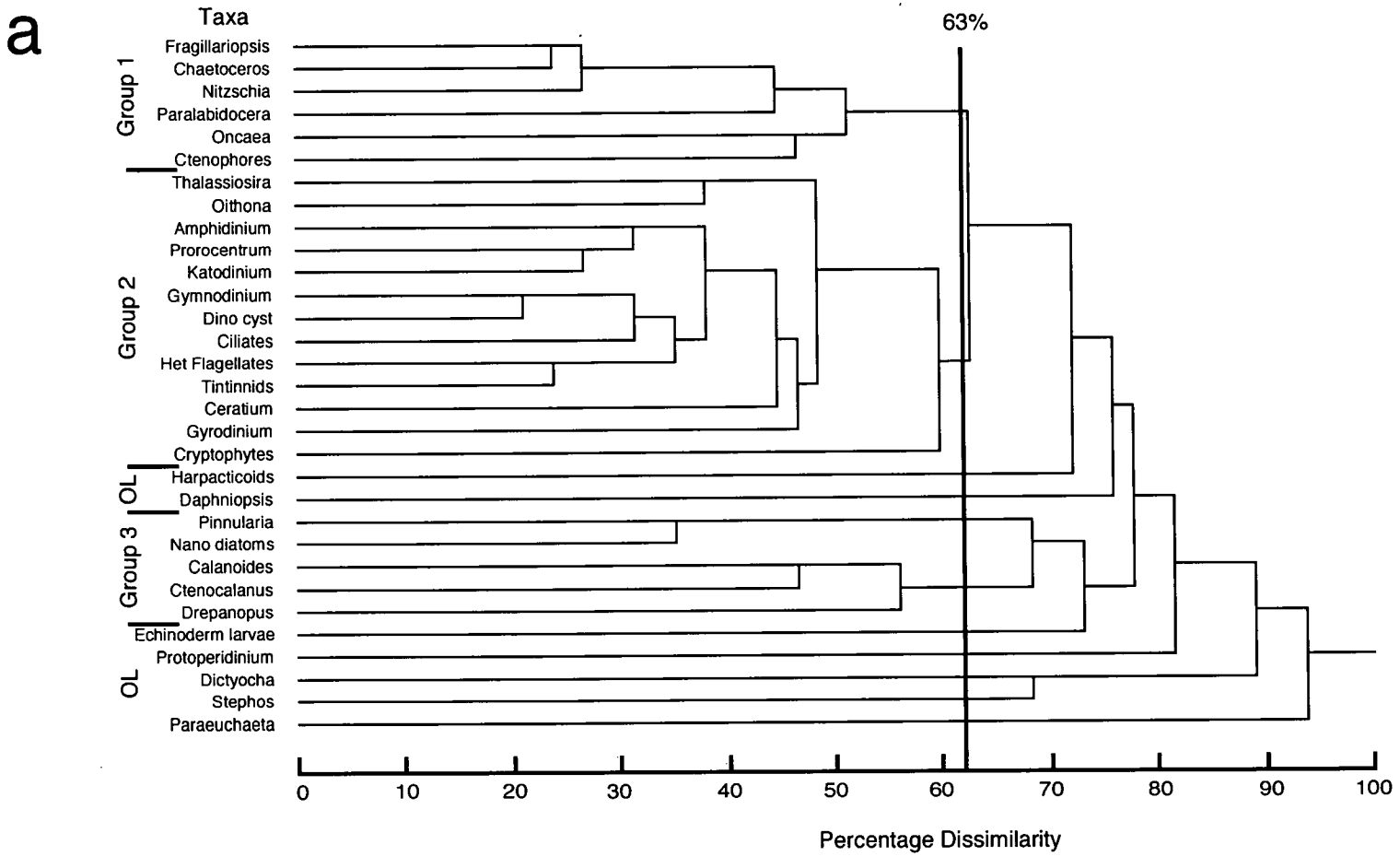


Figure 3.21a. Multivariate analysis of species associations shows the dendrogram of cluster analysis based on the Bray-Curtis dissimilarity index with UPGMA linkage. Only genera and higher taxa are listed, for species information refer to the text. OL = Outlier.

b

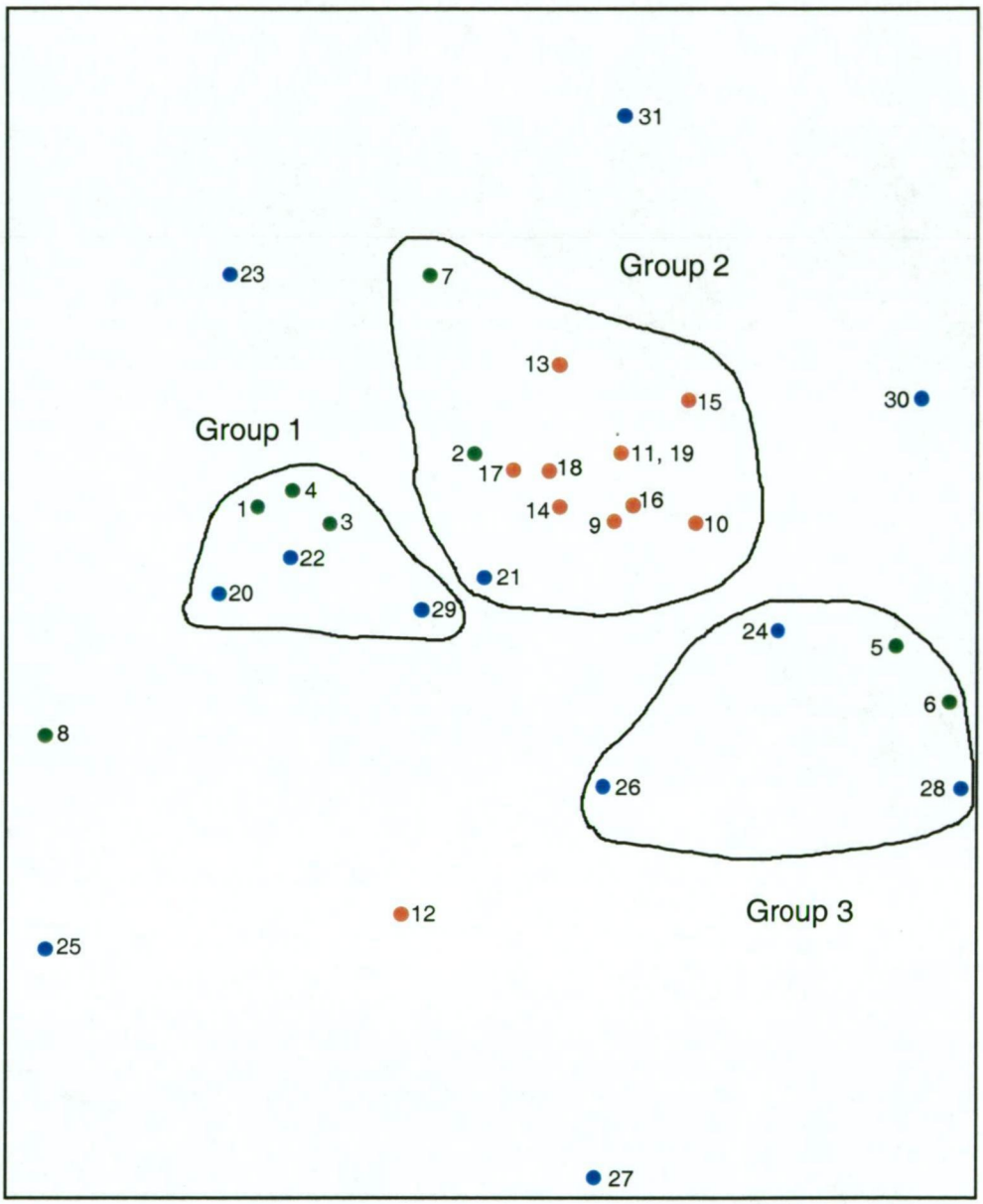


Figure 3.21b. Multivariate analysis of species associations shows the ordination plot of the cluster analysis using NMDS. Colours denote taxa; green = phytoplankton, red = protozoa, blue = metazoa. Numbers denote species as per the text. Axis scales are not shown as they are relative in NMDS.

cryptophyte *G. cryophyllum* were also associated with the aforementioned group. During early February, there was little separation of discrete species groups, but by mid-February the general pattern of species-groupings re-emerged, and the diatom-small copepod group (*sensu* Group 1) and protozoan group (*sensu* Group 2) were again distinct. By late February while Group 1 remained relatively stable, *C. acutus* and other mesozooplankton joined the protozoa in Group 2.

3.4 Discussion

3.4.1 Chlorophyll a concentration and species assemblages in the ice

To my knowledge, the only previous chlorophyll data recorded from the ice in Ellis Fjord was a mean concentration of 5.5 $\mu g\ L^{-1}$ during the winter of 1994 (Swadling 2001). On 3 December I collected two ice cores, and the chlorophyll *a* concentrations were 36.16 $\mu g\ L^{-1}$ and 4.76 $\mu g\ L^{-1}$. The first core appears indicative of high spring / summer production, while the second is indicative of low background levels similar to those recorded during winter. The difference between the chlorophyll *a* concentrations in the two cores, which were taken only a few metres apart, highlights the spatial patchiness of ice-algae in Ellis Fjord. Ice-algal patchiness is a well documented phenomenon and has been reported in the coastal region of the Vestfold Hills (Archer et al. 1996b, Swadling et al. 1997, Swadling et al. 2000a), off the coast of Syowa station (Hoshiai 1985, Watanabe et al. 1990), in the Weddell Sea (Dahms et al. 1990, Garrison & Buck 1991, Schnack-Schiel et al. 1998a, Gunther et al. 1999), and McMurdo Sound (Stoecker et al. 1993).

The ice-algal community was dominated by *P. quadratarea* v. *constricta*, *Pseudonitzschia* spp., and *P. glacialis*. *Pleurosigma* spp. and dinoflagellate cysts were also present. This differs from the ice-algal assemblage reported in December 1992, in which *Entomoneis kjellmanii, Nitzschia stellata, Berkeleya adeliense,* and *Thalassiosira australis* were dominant (McMinn 1996). The difference in algal assemblage could be due to spatial patchiness within the ice. Swadling et al. (1997) found considerable variation in chlorophyll *a* concentrations, and horizontal patchiness of sympagic metazoans, at scales of less than one metre in coastal fast-ice, and, while diving, Kirkwood (1993) observed changes in the under-ice algal assemblages along the fjord.

Differences between this study and that by McMinn (1996) may also be due to interannual variation in ice-algal biomass and species composition in nearby coastal waters (e.g. Gibson et al.1997).

The presence of ice-algae and dinoflagellate cysts in the water column at the end of the season indicated a period of ice-melt. Dinoflagellate cysts are abundant in the sea-ice and are reportedly rarely observed in the water column (Godhe et al. 2001).

3.4.2 Water column production

Chlorophyll *a* concentration first peaked in the water column in mid January at 16.45 $\mu g\ L^{-1}$. However, the major peak occurred on 18 February at all depths, ranging from 13.62 $\mu g\ L^{-1}$ at 40 m, to 27.57 $\mu g\ L^{-1}$ at 10 m. Previous studies have reported variable chlorophyll maxima over spring / summer ranging from 4 $\mu g\ L^{-1}$ (McMinn et al.1995), to 30 $\mu g\ L^{-1}$ (Kirkwood 1993). Peaks have been recorded in late October (Gibson 1998), mid December (McMinn et al. 1995), late December (Kirkwood 1993), early January and mid February (Gibson 1998). This range of chlorophyll *a* concentrations and seasonality of maxima show there is substantial inter- and intra-annual variation in the seasonal biomass of phytoplankton in Ellis Fjord. In general, the summer peak in chlorophyll *a* concentration in Antarctic waters has previously been associated with diatom blooms (Sasaki & Hoshiai 1986, von Bodungen 1986, Socal et al. 1997, Gibson 1998). However, more recently peak chlorophyll *a* concentration has been recorded in conjunction with blooms of nanoplankton and protozoa (Jacques & Panouse 1991, Umani et al. 1998). The peak chlorophyll *a* concentration I recorded in mid January appears associated with the microplanktonic diatoms *F. curta, P. subcurvata* and *T. ambigua*, while the peak in late February was associated with the nanoplanktonic diatom bloom and autotrophic dinoflagellates.

3.4.3 Species succession

3.4.3.1 Phytoplankton

Fragilariopsis curta was the dominant diatom in the water column in early summer. This species is known to appear after ice-melt in response to meltwater stratification (McMinn et al. 2000), and has been observed in fast-

ice (Sasaki & Hoshiai 1986), as well as planktonic communities (Medlin & Priddle 1990). The planktonic diatoms, *T. ambigua* and *P. subcurvata* were also present in the water column during early summer. In the Southern Ocean, it is generally accepted that both meltwater and the release of phytoplankton from the ice promote the spring phytoplankton bloom in the water column (Smith & Nelson 1986). However, recent studies have shown that fast-ice-algae may not contribute substantially to the major phytoplankton bloom in coastal waters (Riebesell et al. 1991, McMinn 1996, Guglielmo et al. 2000, Ishikawa et al. 2001). In this study, ice-algae were observed to rapidly sink through the water column at the beginning of summer (see Chapters 5 & 6). Furthermore, physicochemical data indicates that planktonic phytoplankton blooms can be initiated by the transportation of water masses beneath the ice in Ellis Fjord (Gibson 1998).

In mid-January, freshwater from nearby Lake Druzhby flowed into Ellis Fjord carrying with it the lacustrine crustacean *D. studeri*. By late January, the presence of this crustacean at my sampling site indicated that this freshwater had reached Middle Basin, which presumably led to water column stratification. In the summer of 1994/5 an introduction of warmer less saline water into Middle Basin was observed (Gibson 1999). This corresponded with a decrease in the concentration of chlorophyll *a*, and the dominant phytoplankton changed from diatoms to flagellates (Gibson 1998). While no physicochemical data were collected during my study, the freshwater from Lake Druzhby was presumably warmer and less saline than the resident water in Middle Basin. I likewise observed a decrease in chlorophyll *a* concentration, and a change from a dominance of diatoms to a sudden bloom of the phytoflagellate *G. cryophillum*. Stratification of the water column has been associated with low diatom concentration and cryptophyte blooms (Buma et al. 1992, McMinn et al. 2000). It has been suggested that a lack of turbulence in the stratified layer of the water column results in sedimentation of 'heavy' microplanktonic diatoms thereby allowing the 'lighter' nanoplankton to bloom (Buma et al. 1992, Rodriguez et al. 2001). Stratification of the water column also leads to nutrient depletion, which is also likely to have led to the decline of the diatom bloom observed in upper waters (McMinn et al. 1995). Furthermore, heavy selective grazing by herbivores can result in the succession from microphytoplankton to

nanoplankton (Jacques & Panouse 1991, Carrada et al. 2000, Walsh et al. 2001).

As also shown by Gibson (1999), cryptophtyes appeared to be transported into Middle Basin via an influx of water from the seaward basins (see below). Cryptophytes were first observed in deeper waters during mid-January when the water column appeared to be well-mixed. Stratification, the diatom decline, and increased irradiance in surface waters due to ice-melt appeared to provide ideal conditions for cryptophytes to bloom. Despite this, the bloom was short-lived presumably due to intense grazing (see below) and had declined by early February.

By late February, autotrophic dinoflagellates and the nanoplanktonic diatom *F. pseudonana* bloomed in the upper water column. This coincided with a period of apparent under ice-melt (see 3.4.1 Chlorophyll *a* concentration and species assemblages in the ice). The dinoflagellate population was most likely released into the water column during ice-melt, as the dominant species *P. glacialis* has been commonly recorded in the brine of coastal fast-ice (Stoecker et al. 1991, Stoecker et al. 1992, Montressor et al. 1999, Thomson 2000). Melting fast-ice appears to provide favourable conditions for the growth of *F. pseudonana* (Lancelot et al. 1993, Rodriguez et al. 2001), and blooms have been recorded beneath the ice prior to ice break-out in Ellis Fjord, and the coastal regions off Davis and Syowa stations (McMinn & Hodgson 1993, Ishikawa et al. 2001, Davidson unpubl. data).

In summary, the phytoplankton community in Ellis Fjord comprised a background of microplankton on which nanoplankton blooms were superimposed throughout summer. This is the opposite of the usual scenario for the open ocean, where a background of nanoplankton exists and microplanktonic diatom blooms are seasonally superimposed (Smetacek et al. 1990, Bathmann et al. 1997, Waters et al. 2000). In the open ocean, the zooplankton community is usually dominated by krill and large copepods that clear large diatoms more rapidly than nanoflagellates (Quetin & Ross 1985, Atkinson 1995), whereas in Ellis Fjord, these larger grazers are relatively absent, and small copepods and protozoa dominate (see below). These microzooplankton reportedly feed more efficiently on flagellates than large diatoms (Atkinson 1995, Froneman & Perissinotto 1996), and therefore

presumably contribute to the sporadic blooms of nanoplankton, while exerting less impact on the total diatom concentration (see below).

3.4.3.2 Protozoa

Heterotrophic dinoflagellates (HDIN) were present in low concentration during early summer, but rapidly increased following the cryptophyte bloom, and coincided with the decline in cryptophytes. HDIN are capable of grazing both auto and heterotrophic flagellates, and can reportedly control their production (Becquevort et al. 1992, Lancelot et al. 1993, Tsuda & Kawaguchi 1997, Chapter 6). Therefore, it appears that the stratification of the water column and the cryptophyte bloom provided favourable conditions for HDIN to bloom. In addition, the input of warmer freshwater probably led to some under-ice melt. Heterotrophic dinoflagellates (HDIN) inhabit the brine channels of Antarctic sea-ice and have been recorded in coastal sea-ice adjacent to Ellis fjord (Archer et al. 1996b, Thomson 2000). It is generally accepted that protozoans that inhabit the sea-ice are released into the water column during seasonal ice-melt, resulting in a high biomass of protozoans in near-surface waters (Garrison et al. 1988, Garrison & Buck 1989, Garrison 1991, Nöthig et al. 1991). Therefore the bloom of HDIN observed in mid-summer probably resulted from both the growth of the resident population in the fjord, and release of HDIN from the ice.

Similar to HDIN, ciliates were in low concentration during early summer but began to increase from mid to late summer. This was probably due to several factors including the advent of favourable conditions such as an increase in water temperature that favours excystment (Müller 2002), the change in the composition of available food, and the seeding of ciliates from the ice. Ciliates and heterotrophic flagellates inhabit the brine channels in the ice (Stoecker et al. 1990), and can account for up to 50% of the protist biomass before ice break-out (Stoecker et al. 1993). The peak concentration of ciliates followed that of HDIN. Ciliates are able to graze a wide range of taxa, including dinoflagellates, diatoms, and flagellates (Pierce & Turner 1992, Gustafson et al. 2000), and these potential food sources were all available in the water column. However, in late summer, tintinnids were observed to primarily graze the nanoplanktonic diatom *F. pseudonana*.

HDIN and ciliates exert considerable grazing pressure on diatoms, and can control diatom blooms in Antarctic waters (Burkill *et al.* 1995, Klaas 1997a,b, Tsuda & Kawaguchi 1997). Diatoms have been observed within cells of HDIN (Nöthig et al. 1991) and in their faecal pellets (Buck et al. 1990). The occurrence of HDIN in early February coincided with a further decline in the concentration of microplanktonic diatoms. Furthermore, faecal pellets resembling those produced by HDIN were observed to contain diatoms (see Chapter 4). Therefore, in addition to sedimentation, HDIN grazing most likely contributed to the maintenance of low concentrations of microplanktonic diatoms observed from mid to late summer.

Previous studies in Ellis Fjord did not explore the effect of grazing on protistan succession, presumably because they reported that protozoa were not numerically significant (McMinn and Hodgson 1993, Gibson 1998). However, there is increasing recognition that despite their lower abundance, protozoan grazing can impact considerably upon phytoplankton concentration and species assemblages (Garrison and Buck 1989, Bjørnsen & Kuparinen 1991, Burkill et al. 1995, Klaas 1997a,b). In this study, it appears that even in low concentration, protozoan grazing could exceed phytoplankton production, indicating that protozoa played a substantial role in determining the succession of the phytoplankton community (see Chapter 6).

Heterotrophic flagellates were in high concentration from mid to late summer. Heterotrophic flagellates are important components of the microbial loop and graze bacteria, nanoplankton and particulate organic matter (POM) (Fenchel 1988, Garrison and Buck 1989). Melting fast-ice initiated much heterotrophic activity during February that led to a high concentration of faecal pellets in the water column (see Chapter 4). Small faecal pellets and detrital matter that are recycled in the water column provide a substrate for bacterial growth thereby facilitating increased bacterial production (Roman et al. 1988, Bianchi et al. 1999). Furthermore, bacterial production has been reported to increase after ice melt (Kottmeier and Sullivan 1990, Delille et al. 1995). Therefore it is likely that a high bacterial biomass supported the growth of heterotrophic flagellates.

3.4.3.3 Metazoa

Small copepods

Small copepods were numerically dominant in the fjord over summer. *Paralabidocera antarctica* was abundant in mid December reaching a maximum of 16 m^{-3} in the upper 5 m of the water column. Peaks of *P. antarctica* ranging from 41 to 124 m^{-3} beneath the ice in December were previously reported in Middle Basin over three summer seasons (Kirkwood 1993). *Paralabidocera antarctica* has also been reported in high concentration beneath the ice in early summer in the coastal regions off Davis station (Swadling 1998) and Syowa station (Tanimura et al. 1984, Tanimura et al. 1986). The species exhibits a one year lifecycle and undergoes much of its early development in the ice (Tanimura et al. 1996), where it feeds on ice-algae (Hoshiai et al. 1987), presumably all year round (Swadling et al. 2000b). Copepodids are released from the ice during early summer, resulting in a sudden pulse of individuals to the water column, and rapidly develop into adults that die after spawning (Tanimura et al. 1996).

Following the peak of *P. antarctica* in the upper water column during December, the population became distributed throughout the water column during January, declined during February and was absent by early March. A similar pattern was observed in previous summers in Middle Basin (Kirkwood 1993) and also in coastal waters off Syowa station (Tanimura et al. 1996). I suggest the decline in abundance was most likely due to natural mortality of copepodids, and/or predation. Ctenophores and fish are potential predators of *P. antarctica* (Hoshiai and Tanimura 1981, Kirkwood 1993) and both were present in the fjord (see below). The absence of *P. antarctica* in early March appears to be due to post-reproductive mortality of adults, and nauplii do not occur until late March (Tanimura et al. 1996).

Oncaea curvata and *O. similis* often dominate copepod abundance in Antarctic coastal waters (Hopkins 1985, Schnack et al. 1985, Tanimura et al. 1986, Tucker & Burton 1990, Hopkins et al. 1993, Swadling 1998). Similarly, I found *O. curvata* dominated copepod abundance in Middle Basin. The population increased from late December to a peak of 631 m^{-3} in mid January. Abundances of *O. curvata* in Middle Basin have ranged from 400 to 1500 m^{-3} in previous summers (Kirkwood 1993), and in other Antarctic

waters abundances are reportedly highly variable, ranging from 100 to 5200 m^{-3} (Fukuchi & Tanimura 1981, Tanimura et al. 1986, Tucker and Burton 1990, Metz 1995, Swadling 1998). Moreover, there appears to be no seasonal pattern of abundance as peaks in abundance have been reported throughout the year (Fukuchi & Tanimura 1981, Tanimura et al. 1986, Tucker & Burton 1990, Swadling 1998).

The diet of *O. curvata* remains equivocal, however diatoms (including nanoplankontic forms) and detritus have been reported from gut content analyses (Hopkins 1985b, Hopkins 1987, Hopkins and Torres 1989). The single feeding study by Metz (1996) confirmed that diatoms are acceptable food for *O. curvata* females. However, a preference was shown for non-motile food, such as large aggregates and *Phaeocystis* colonies (Metz 1996, 1998). Although the species is not solely herbivorous, their lifecycle appears coupled to the seasonality of the phytoplankton bloom (Metz 1996).

In the present study, the distribution and abundance of *O. curvata* followed that of the microplanktonic diatom bloom that occurred from 11 January to 1 February (Figures 3.3 & 3.10). Furthermore, *O. curvata* appeared to migrate to deeper waters, or could have been transported to depth via attachment to aggregates during sedimentation of the bloom (Ohtsuka & Kubo 1991, Paffenhöfer 1993). Females with egg sacs were found in deeper waters in the Bellingshausen Sea (Metz 1996), and Metz (1995) concluded that the species undergoes ontogenetic migration. All lifestages have been reported throughout the year (Kirkwood 1993, Metz 1996, Tanimura et al. 1997), and this led Kirkwood (1993) to conclude that there appears to be no consistent seasonal cycle of abundance of *O. curvata* in the Antarctic coastal marine environment. However, it appears that a period of reproduction has been recorded during several summers. In Middle Basin copepodids dominated the population structure, except in early January when a peak of *O. curvata* adults was observed prior to an increase in copepodids in February (Kirkwood 1993). This pattern was also observed in the coastal population (Swadling 1998), suggesting that *O. curvata* reproduced during early summer. Reproduction of *O. curvata* during summer has also been reported in surface waters of the Weddell Sea (Metz 1995, 1996). Therefore, it appears that *O. curvata* produces a summer cohort, although the year round presence of all lifestages in the water column suggests reproduction is not confined to

a distinct seasonal cycle (i.e. there is continuous recruitment). The decline and migration of *O. curvata* coincided with an increased abundance of dinoflagellates in upper waters. It has been shown that dinoflagellates can prey upon copepod eggs and nauplii (Elbrächter 1988, Jeong 1994). Therefore, following mating, females may migrate to deeper waters to spawn, thereby avoiding predation of their offspring. The low abundance of *O. curvata* in upper waters could also result from predation by ctenophores (see below).

The abundance of *O. similis* recorded in this study was generally an order of magnitude lower than that of *O. curvata*. Lower abundances of *O. similis* have previously been reported during summer in Ellis Fjord (Kirkwood 1993) and adjacent coastal waters (Swadling 1998). Furthermore, it appears that *O. curvata* dominates in sheltered coastal waters, while *O. similis* dominates in more turbulent waters such as the open ocean (Hopkins 1985b, Tucker & Burton 1990, Kirkwood 1993, Metz 1995, Swadling et al. 1997, Atkinson 1998, Schnack-Schiel et al. 1998b, Ward & Shreeve 1999, Atkinson & Sinclair 2000, Dubischar et al. 2002). This difference in distribution may be related to differences in the behavioural ecology of the two species. *Oncaea* spp. are reported to show near-continuous motion (Paffenhöfer 1993), and while observations by Metz (1998) report that *O. curvata* is lethargic, I observed *O. curvata* to be highly motile (Beaumont unpubl data). In contrast, *O. similis* has poor swimming ability, moves infrequently, and the copepodites of this species remain motionless for long periods (Drits & Semenova 1984, Paffenhöfer 1993). In addition, *O. similis* appears more epipelagic than *O. curvata* in Antarctic waters (Hopkins 1985a, González et al. 1994a, Metz 1995, Atkinson et al. 1996, Schnack-Schiel et al. 1998b, Ward and Shreeve 1999, Atkinson & Sinclair 2000). *Oithona similis* is omnivorous, feeding on varied food sources that are abundant at the ice-water interface (see below), and it has been suggested that this species may be ice-associated, as it feeds on both bottom-ice-algae and faecal pellets from sympagic grazers, and is the main prey of the ice-fish *Pagothenia borchgrevinkii* (Hoshiai et al. 1991, Atkinson 1995, see below). Turbulence may foster high abundances of *O. similis* by maintaining populations in upper waters where food is abundant. In sheltered waters this species may be unable to control its vertical distribution in the water column, due to its poor swimming ability. Therefore, it may be unable to fully utilise the

available food. In contrast, it appears that in sheltered waters *O. curvata* is able to prosper. While much remains to be known regarding this species' diet and feeding ecology, *O. curvata* has been observed attached to aggregates in the water column, and the motility of this species may enable it to capitalise on such episodic food sources (Ohtsuka & Kubo 1991, Paffenhöfer 1993, Metz 1996).

All lifestages of *O. similis* have been found year-round indicating mixed cohorts and overlapping generations (Fransz & González 1995). However, highest egg production has been recorded in spring (Sabatini & Kiørboe 1994), and the main development of copepodids between January and May (Fransz & González 1995). The abundance of *O. similis* fluctuated in early summer and peaked in early February. This peak coincided with that of HDIN, and followed the bloom of cryptophytes. *Oithona similis* is reported to feed on flagellates (Drits & Semenova 1984, Sabatini & Kiørboe 1994, Nakamura & Turner 1997), dinoflagellates and ciliates (Nakamura & Turner 1997), faecal pellets (González & Smetacek 1994), and diatoms (Hopkins 1987). These potential food sources were all available in the water column during February, yet the abundance of *O. similis* proceeded to decline in the upper 5 m of the water column. The neritic fish, *Trematomus newnewsii* was observed on numerous occasions directly beneath the ice during the sampling period. Analysis of the stomach contents of *T. newnesii* fry collected off Syowa station showed *O. similis* comprised over 50% of the prey (Hoshiai and Tanumura 1981). Therefore, *O. similis*, may also have been heavily preyed upon in Ellis Fjord.

Harpacticoid copepods were not common in Middle Basin, but showed a brief occurrence during mid January. Kirkwood (1993) reported varying abundance of harpacticoids throughout the year in Ellis Fjord with highest abundances occurring in the landward basins. The abundance of harpacticoids I recorded was very low compared to those previously reported in Middle Basin, and reflects abundances observed in the seaward basins (Kirkwood 1993). Furthermore, harpactioids have been recorded in high abundance from the ice near Ellis Narrows, but were absent from the ice of upper meromictic basins (Swadling 2001). I suggested previously (see 3.4.3.1 Phytoplankton) that an influx of coastal seawater reached Middle Basin in mid January, and thus propose that harpacticoids could have been

transported into Middle Basin. In addition, the population could also have been released from the ice via under-ice melt that occurred from mid to late January. Further evidence of the influence of both seawater influx and/or ice-melt is provided by the presence of *C. citer*. This small copepod was not observed in the fjord by Kirkwood (1993), but is a common coastal species that may be associated with the sea-ice (Swadling 1998).

Large copepods

The large calanoid copepod *C. acutus* is a common species in the deeper oceanic waters of Prydz Bay (Hosie 1994a,b, Hosie and Cochran 1994). It has been recorded in coastal waters off Davis station in summer but is thought to be an offshore migrant (Tucker and Burton 1990, Swadling 1998). The lifecycle of *C. acutus* is reported to be 1-2 years (Atkinson et al. 1997).

Calanoides acutus was occasionally present in the lower water column during January. However, the main population of approximately 32 m^{-3}, occurred during February when *C. acutus* appeared to migrate to upper waters. Kirkwood (1993) observed a similar increase of *C. acutus* in mid summer and concluded this was due to an influx of new individuals from outside the fjord. Moreover, Kirkwood (1993) suggested the population was not self-maintaining, and recent evidence suggests that *C. acutus* is unable to reproduce in ice-covered waters (Voronina et al. 2001). Consequently, the interannual variation in the abundance of *C. acutus* in Ellis Fjord is coupled to that of the summer sea-ice melt and water flow through Ellis Narrows.

Calanoides acutus is mostly herbivorous (Schnack et al. 1985, Atkinson et al. 1996) and the species abundance and lifecycle are keyed to the phytoplankton bloom (Atkinson & Shreeve 1995). However, the presence of *C. acutus* in the fjord was determined by the timing of the water input that occurred after the bloom of microphytoplankton. Protozoa are reported to be an important source of copepod nutrition (Sherr & Sherr 1988, Gifford 1991, Sanders & Wickham 1993, Nakamura & Turner 1997), particularly after the spring bloom when primary production is dominated by nanoplankton (Sherr et al. 1986, Stoecker & Capuzzo 1990). Feeding studies have shown that *C. acutus* will graze dinoflagellates and ciliates (Atkinson 1995) and ciliates were preferentially grazed over nanoplanktonic diatoms (Atkinson 1996). *C. acutus* increased in abundance and migrated to upper waters

during late summer, when dinoflagellates, ciliates, and nanoplanktonic diatoms dominated the upper water column. Therefore, it is likely that in the relative absence of microplanktonic diatoms, protozoa may have provided a suitable food source for *C. acutus*.

Drepanopus bispinosus is a common species in saline lakes and inlets of the Vestfold Hills (Bayly 1986, Eslake et al. 1991, Wang 1995), and has only been recorded once, in very low abundance from the coastal region (Tucker 1983). Both nauplii and adult females occur in the water column during summer (Bayly 1986). *Drepanopus bispinosus* has only been recorded previously in the upper basins of Ellis Fjord (Kirkwood 1993). Highest abundances (1200 m^{-3}) were reported in the most landward basin (Small Meromictic Basin) with much lower abundances (8 m^{-3}) in the more seaward basin (Large Meromictic Basin). Similarly, I recorded low abundances (9 m^{-3}) in Middle Basin in late summer. This supports my earlier suggestion, based on the occurrence of the lacustrine *D. studeri*, that water from upper basins reached Middle Basin during late summer (see 3.4.3.1 Phytoplankton). Like *D. bispinosus*, *D. studeri* was previously only reported in the upper basins (Kirkwood 1993). Therefore it appears that during summer 1997/98 there was a greater input of water, and subsequent along-fjord mixing, from both coastal (see above) and lacustrine sources.

The extent of water input to Ellis Fjord is dependent on the degree of ice-cover at Ellis Narrows (seaward entrance) and Ellis Rapids (landward entrance). Both of these are shallow entrances (< 3 m deep) and, therefore, are easily restricted by ice-cover. Variations in the degree of summer ice-melt leads to variations in the amount of freshwater input from the upper freshwater lakes and seawater input from the adjacent coastal waters (Kirkwood 1993, Gibson 1999). I observed greater ice-melt over summer 1997/98 than that observed in previous summers (Kirkwood unpubl. data) and consequently greater water input and along-fjord mixing. The variation in annual ice-formation and mixing in the fjord has been discussed by Gibson (1999), who concluded that changes in these physical processes would influence water chemistry and biology along the fjord. I have examined the distribution and abundance of biota in Ellis Fjord in light of individual species' ecologies and changes in the physical environment. Changes in the physical and biological characteristics recorded in Ellis Fjord

suggest that interannual variation in ice-melt and water flow drives the large interannual variation in species abundances and community succession (Kirkwood 1993, Gibson 1998, this study).

Other metazoa

Sudden peaks of echinoderm larvae have been recorded in mid summer in Ellis Fjord (Kirkwood 1993) and adjacent coastal waters (Swadling 1998). Echinopluteus larvae belonging to *Sterechinus neumayerii* (Meisner) were reported as the most abundant larval form (Kirkwood 1993). *Sterechinus neumayerii* is the most widespread benthic species in the fjord (Kirkwood & Burton 1988), and is reported to be the most abundant sea urchin in shallow Antarctic waters (Bosch et al. 1987, Brey 1991, Brey & Gutt 1991). The species spawns from spring to early summer (Bosch et al. 1987, Pearse et al. 1991, Brockington & Clarke 2001). Embryos and early larval stages have been recorded in the water column from November to December (Rivkin et al. 1986), while echinopluteus larvae have been recorded from January to February (Kirkwood 1993, Swadling 1998, Stanwell-Smith et al. 1999, this study).

There has been debate over whether temperature or food availability initiates spawning (Pearse and Giese 1966, Yakovlev 1984, Bosch et al. 1987, Pearse et al. 1991, Hoegh-Guldberg & Pearse 1995, Stanwell-Smith & Peck 1998, Brockington & Clarke 2001). The peak of echinopluteus larvae in Middle Basin coincided with the occurrence of exclusively freshwater crustaceans, indicating an influx of water into the fjord through Ellis Rapids. Sudden peaks of echinoid larvae in previous summers also coincided with peak water flow through Ellis Rapids (Kirkwood 1993). Summer warming melts snow and ice in the upper catchment, which leads to water flow from the freshwater lakes through Ellis Rapids and into the fjord. This warming also causes melting of the fast-ice that covers the fjord. Furthermore, the abundance of echinoid larvae in adjacent coastal waters also appears linked to ice-melt during summer (Swadling 1998). Therefore, it appears that surface warming directly promotes larval development, or that surface warming and the resulting ice-melt influences food availability in the water column, leading to peak abundances of echinoid larvae in near-surface waters.

In the present study, the influx of water instigated a change in community structure from large diatoms to an abundance of nanoplankton, dinoflagellates, and detritus. Diatoms and dinoflagellates are suitable food for echinoderm larvae (Strathmann 1971). However, the larvae appear to feed most efficiently on nanoplankton (Rivkin et al. 1986). Furthermore, laboratory studies have shown that echinoid larvae can feed almost exclusively on bacteria and detritus (Lessard & Rivkin 1986, Rivkin et al. 1986). Clearance rates of echinopluteus on protists are reported to be an order of magnitude lower than that of small copepods (Strathmann 1971), however their clearance rates on detritus occupy a similar range (Lessard & Rivkin 1986, Rivkin et al. 1986). Therefore echinoid larvae may contribute to the consumption of detritus, although their grazing impact on protists is likely to be minimal.

A ctenophore, probably *Callianira cristata,* was abundant throughout summer, predominantly in the upper water column. Large interannual variation in the abundance of *C. cristata* has been reported in Ellis Fjord (Kirkwood 1993). Adults were recorded in low abundance during two previous summers, however in summer 1985/86 the ctenophore dominated the zooplankton biomass (Kirkwood 1993). *Callianira cristata* has been recorded in high abundance from the coastal region (Swadling 1998) and a saline lake in the Vestfold Hills (Bayly 1986). Despite the widespread abundance of ctenophores in the world's oceans there is a lack of information on their biology and ecology (Mills 1995). They are generally considered to be carnivores (Reeve & Walter 1978), and are known to prey on copepods and other metazoa (Harbison et al. 1978, Mills 1995).

Callianira cristata was observed to eat large numbers of *D. bispinosus* (Bayly 1986) and *P. antarctica* (Wang pers. comm. in Kirkwood 1993) in a saline lake in the Vestfold Hills. *Drepanopus bispinosus* was not highly abundant in Ellis Fjord, therefore *P. antarctica* was suggested as the most likely food source (Kirkwood 1993). I suggested earlier that the low abundance of *P. antarctica* in summer could be due partly to predation (see above), although the low abundances are most likely due to post-spawning mortality. Additionally, the ctenophore distribution appeared to follow that of *O. curvata* from early to mid summer. It has been shown for a range of prey concentrations that ctenophore ingestion is proportional to food concentration (Reeve and

Walter 1978). Therefore it seems likely that *O. curvata* contributed to the ctenophore diet. The abundance of *O. similis* increased from mid to late summer, and this copepod species may constitute prey for ctenophores. While it is probable that small copepods constituted the main ctenophore prey, it has also been suggested that phytoplankton and detritus may contribute to the diet of cydippid ctenophores (Reeve and Walter 1978). Dietary knowledge of Antarctic ctenophores is severely lacking, therefore I can only speculate on the prey of the ctenophore present in Middle Basin during summer.

Potential predators of ctenophores are the large ctenophores *Beroe* spp. (Barnes 1987) and nototheniid fish (Pakhomov 1993). I noted earlier the presence of *T. newnewsii* in the fjord (see above). While *Beroe* spp. have not been recorded in Ellis Fjord, they have been reported from adjacent coastal waters. An influx of coastal seawater occurred during my sampling season and therefore it is possible that *Beroe* spp. could have been transported into the fjord (Kirkwood 1993). The presence of these predators may also influence ctenophore distribution and abundance in the fjord over summer.

3.4.4 Ecological interactions and community succession

I have examined changes in community composition in relation to the physical environment and species' life-history strategies. Subsequent statistical analyses allowed me to identify trophic groups, and their vertical distributions and succession over summer. Based on this information, I have constructed a temporal food web diagram (Figure 3.22) that summarises these ecological interactions and community succession.

In early summer, ice-algae on the underside of the ice represented a major source of primary production, indicated by chlorophyll *a* concentrations up to 36 μg Chl *a* L^{-1}. This provided a large food source for epontic (under-ice) grazers such as small copepods. Additionally, a planktonic bloom of diatoms was present in the upper water column. I reported that the dominant small copepods will graze diatoms and the majority of copepods were present in upper waters. Furthermore, these small copepods were possibly preyed upon by ctenophores and fish. Reverse cluster analysis identified microplanktonic diatoms, small copepods and ctenophores as a trophic

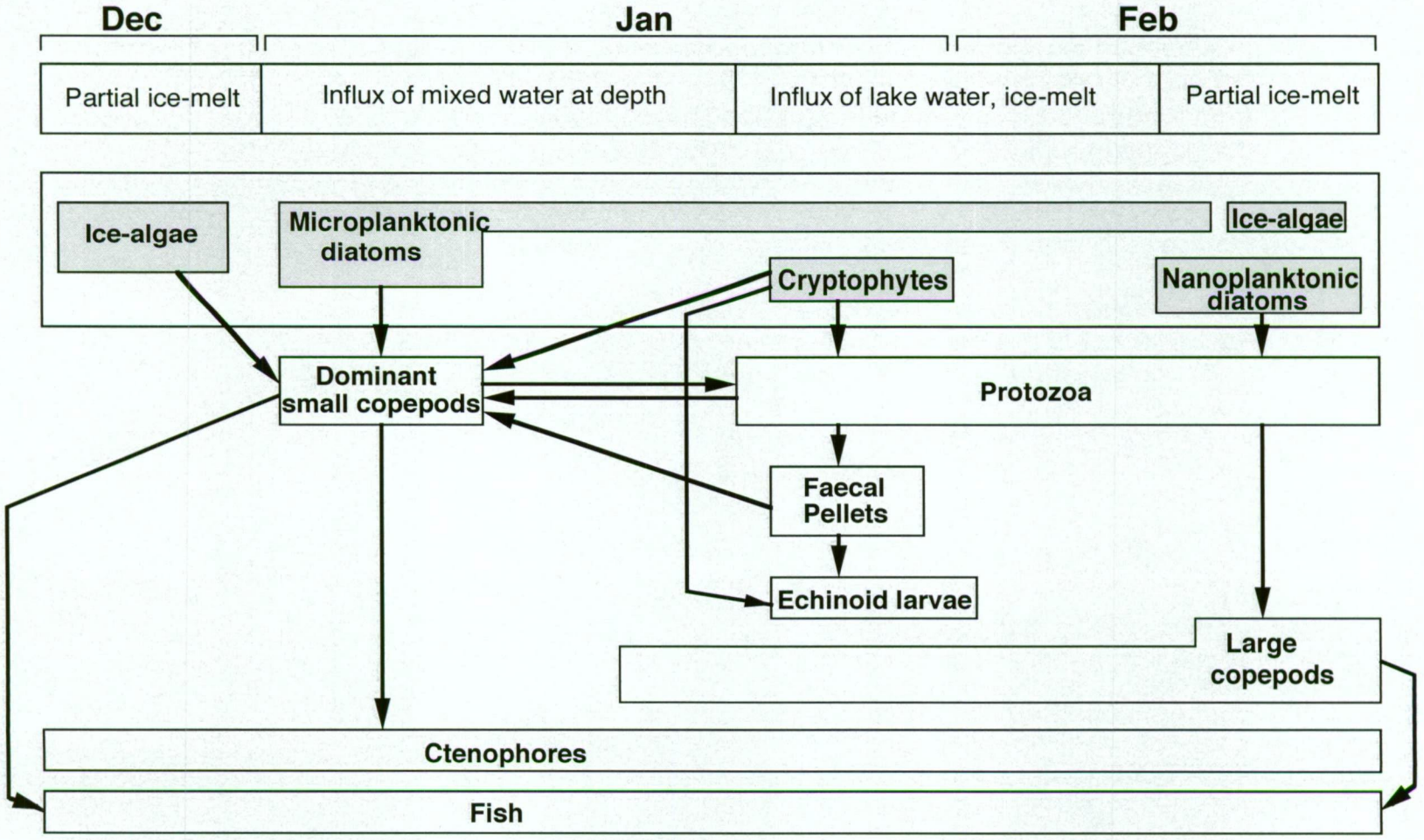


Figure 3.22. A temporal food web diagram summarising the ecological interactions and community succession during summer 1997/98 in Ellis Fjord.

group. (Note: fish were not quantitatively sampled, therefore they were not included in the analysis). This diatom - small copepod - ctenophore / fish food chain is typical of a 'classical' food web (Fenchel 1988). When this classical food web was operative in early summer it appears that species distributions in the water column were governed by the concentration of diatoms in upper waters. Therefore, the vertical distribution of biota throughout the water column was not uniform.

Towards mid-summer, the diatom concentration in upper waters declined. This decline coincided with observations of under-ice melt that presumably led to water column stratification and facilitated an increase in protozoa due to release of protozoa from the ice and enhanced *in situ* planktonic growth. Therefore it would appear that the decline in diatoms resulted from an increase in grazing pressure due to the influx of protozoa, and sedimentation of diatoms from stratified waters. The absence of diatoms allowed a cryptophyte bloom in the stable melt-water beneath the ice. This succession, from diatoms to cryptophytes, is common in Antarctic waters (Jacques & Panouse 1991, Walsh et al. 2001), and has previously been observed in Ellis Fjord (McMinn & Hodgson 1993, Gibson 1998). Moreover, it has been suggested that the succession from diatoms to cryptophytes promotes a change in the dominánt trophic structure from a classical fuelled food web to a microbial one (Jacques & Panouse 1991).

The cryptophyte bloom was short-lived. This was most likely due to grazing by protozoa, although it is possible that *O. similis* and echinoid larve also graze cryptophytes. The peak abundance of *O. similis* coincided with that of heterotrophic dinoflagellates and statistical analysis showed *O. similis* was borderline between the protozoan and classical trophic groups. Additionally, statistical analysis of species associations in mid summer showed that the small copepod and protozoan trophic groups merged. This suggests that *O. curvata* and *O. similis* could compete with protozoa for the same food source, that protozoa could prey upon small copepods, or that *O. similis* could be grazing protozoa. Additionally, *O. similis* exhibits coprophagy (González and Smetacek 1994) and *O. curvata* will feed on gelatinous aggregates (Metz 1996). Therefore, protozoan faecal pellets may also contribute to the diet of these small copepods. Faecal pellet production and sloppy feeding by small copepods could also indirectly contribute to protozoan nutrition by fuelling

the microbial loop (Azam 1998, Turner 2002). Therefore, the interactions between protozoa and small copepods are varied, ranging from competition to mutual predation and reciprocal scavenging. Such complex interactions between these abundant grazers presumably led to the more homogeneous vertical distribution of biota in the water column I observed during mid summer.

Copepods are generally considered part of the classical food web, largely due to the morphologies and life-history strategies of large copepods. However, small copepods possess different morphologies, behaviour, and life-history strategies (Paffenhöfer 1993, Williams et al. 1994). Large copepods are predominantly dependent on diatoms for food. Their reproduction is timed to coincide with the summer diatom bloom and many species undergo diapause during winter. Whereas small copepods are capable of eating a variety of food, including flagellates and nanoplankton, and appear capable of reproduction all year round. Consequently, small copepods can be a 'classical' consumer when diatoms are abundant, but, in the absence of diatoms, they can utilise the microbial food web and thereby occupy a similar trophic level to protozoa.

Protozoa are reported to link nanoplankton to higher trophic levels. However, I suggest small copepods may also provide an important link between the microbial and classical food webs, particularly in Antarctic coastal waters where they dominate copepod abundance and where primary production is seasonally limited. Year-round studies of Ellis Fjord and the adjacent coast have generally shown that protozoans and small copepods reach maximum abundance in autumn after the summer diatom bloom (Tucker & Burton 1990, Kirkwood 1993, Swadling 1998, Gibson 1999). Therefore, investigations of the interactions between protozoans and small copepods during autumn may provide an insight into plankton community structure and particle flux beyond the summer period of production.

From mid to late summer, the presence of ice-algae and abundance of autotrophic dinoflagellates indicated further under-ice melt. Moreover, a bloom of nanoplanktonic diatoms developed beneath the ice, and such blooms have previously been associated with meltwater stratification (Lutter et al. 1989, Umani et al. 1998, Ishikawa et al. 2001). The abundance of

diatoms and dinoflagellates provided an ample food source for ciliates that rapidly increased in abundance during late summer. The population of large copepods also increased, although their overall abundance remained low, and they appeared to migrate to upper waters to graze protozoa. Therefore, in late summer, as small copepods declined and protozoa became highly abundant, large copepods became more prominent and the dominant copepod / protozoan relationship changed from one of competition to that of predator / prey. Ctenophores remained abundant in the upper water column and both ctenophores and fish potentially preyed upon large copepods. This resulted in a return to the more classical paradigm with protozoa linking the microbial food web to these higher trophic levels.

In summary, there was a shift in trophic structure from early to mid-summer in Ellis Fjord from a classical fuelled food web based on microplanktonic diatoms to a microbial fuelled food web based on nanoplankton. This shift in trophic structure, coupled with an increase in protozoa, appeared to elicit a change in the trophic behaviour of small copepods from that of a classical consumer to one of a microbial consumer. By late summer, the decline in small copepods and the presence of large copepods, that graze protozoa, promoted the protozoa as the main microbial consumer that linked the microbial and classical food webs (Sherr et al. 1986, Stoecker and Capuzzo 1990, Gifford 1991, Burkill et al. 1995, Klein Breteler et al. 1999).

The shift to a food web fuelled by the microbial loop over summer has previously been associated with phytoplankton succession resulting from melt-water induced stratification of the water column (Jacques & Panouse 1991, Nöthig et al. 1991, Nielsen et al. 1993). Additionally, in Ellis Fjord, the seasonal ice-melt governs water input to the fjord, which can affect phytoplankton succession by transporting species in and out of the fjord as well as the distribution of protozoan and metazoan biomass (Gibson 1999). The physical dynamics of ice-melt and water input also indirectly influence the distribution and abundance of protozoan and metazoan food, which can affect species behaviour and susbequent trophic relations. These relations are paramount in determining whether matter sinks or is retained in the water column, and thereby in determining the magnitude of biogenic particle flux (Le Fèvre *et al.* 1998, Wassmann 1998).

Chapter 4

Ultrastructure, morphology and flux of microzooplankton faecal pellets in an east Antarctic fjord[1]

4.1 Introduction

The transfer and vertical flux of photosynthetically fixed carbon in the oceans influences atmospheric - ocean carbon flux and consequently global climate (Falkowski et al. 1998, Rivkin & Legendre 2001). Zooplankton play an important role in carbon cycling by packaging planktonic material into faecal pellets that contribute to respiration and nutrient regeneration, or vertical flux (Noji 1991, Banse 1995a, Le Fèvre et al. 1998, Wassmann 1998, Turner 2000). However, the contribution by proto- and metazoa to vertical flux, particularly by individual species, is poorly understood. Small copepods have recently been recognised as being highly abundant in Antarctic waters, contributing substantially to zooplankton biomass and production (Fransz & González 1995, Swadling et al. 1997, Metz 1998, Atkinson & Sinclair 2000). Protozoa are fundamental to the function of the microbial loop, through which most of the carbon flows in marine ecosystems (Fenchel 1988, Froneman & Perissinotto 1996, Azam 1998). The production of pellets by small copepods has been recognised for some time and these pellets are reportedly respired in near-surface waters (Smetacek 1980, Wassmann et al. 1994, Bathmann 1996, González et al. 2000). In contrast, the production and flux of protozoan pellets have only recently been considered despite the fact that they can be of equivalent size to those produced by small copepods (Buck & Newton 1995, Gowing et al. 2001).

To understand the regulation of pellet flux better it is necessary to determine the ecology and trophodynamics of key species (Verity & Smetacek 1996, Wassmann 1998, MZC2 2001). Studies investigating vertical flux using

[1]Published in part as Beaumont KL, Nash GV, Davidson AT (2002) Ultrastructure, morphology and flux of microzooplankton faecal pellets in an east Antarctic fjord. Marine Ecology Progress Series 245:133-148. Authorship acknowledges technical assistance by GV Nash, and statistical and grammatical assistance by AT Davidson.

sediment traps have seldom simultaneously determined the plankton in the overlying water column. This has led to classification of faecal pellets being ill-defined and their origins being largely unknown or presumed.

Marine environments that have low species richness, such as Ellis Fjord, provide the opportunity to investigate fine-scale interactions and the role of key species in vertical flux (Trull et al. 2001). In this study, I investigate the distribution, abundance and linkage between microzooplankton and small pellets, from Ellis Fjord. I examine the morphology and ultrastructure of faecal pellets using light and scanning electron microscopy, and consider the extent to which species-specific trophodynamics and pellet ultrastructure affect the contribution by microzooplankton to vertical flux.

4.2 Methods

4.2.1 Field sampling

Holes were drilled in the sea-ice using a 20 cm auger attached to a Jiffy drill. Net hauls were taken to sample the zooplankton community, and samples were preserved in Steedman's solution as per Chapter 3 (see 3.2.1 Sampling).

A 2 L Kemmerer bottle was used to obtain water samples at approximately weekly intervals to examine the protistan community in the water column (see Chapter 3, 3.2.1 Sampling).

Sediment traps were deployed through 20 cm diameter holes drilled through the ice cover of Ellis Fjord. A total of 12 holes (three square grids of four holes) were drilled. The distance between the holes was approximately 2 m. A sediment trap was suspended in each of the four holes at a depth of 5, 10, 20 or 40 m. This sequence was repeated in the remaining two grids, providing three replicate samples for each depth. As per the recommendations from Chapter 2, the traps consisted of a cylindrical section (internal diameter 65 mm, 6:1 aspect ratio) connected to a funnel that tapered into a cylindrical collector tube after Bloesch & Burns (1980) and Rosa et al. (1994). The traps were filled with 0.2 μm filtered seawater to which 50 g L^{-1} sodium chloride and 6.5×10^{-4} g L^{-1} mercuric chloride had been added to minimise loss of material during retrieval and *in situ* bacterial production

(Knauer et al. 1984, Lee et al. 1992). The traps were retrieved weekly, fresh sample tubes were attached immediately and the traps redeployed. The fixed samples, containing faecal pellets, were placed in a dark, insulated container, and transported to the laboratory at Davis station.

4.2.2 Laboratory methods and statistical analyses

4.2.2.1 Sample preparation and light microscopy

The laboratory methods used to determine the concentrations of proto- and metazoa have been described in Chapter 3 (see 3.2.1 Sampling).

The samples in the collector tubes of the sediment traps, which had been fixed in a mercuric chloride / brine solution, were gently mixed, and the total sample (around 200 ml) from each replicate decanted and split into three for the following analyses: 80 ml for the analysis of faecal pellets (this study), 40 ml for the examination of protists (see Chapter 5), and 80 ml for POC analysis (see Chapter 6).

Samples for the analysis of faecal pellets were settled in Utermöhl sedimenting chambers, and examined using an inverted microscope to identify and enumerate faecal pellets. Only two replicates were analysed due to the time involved in such detailed analyses. Faecal pellets were classified into four categories based on pellet descriptions from the literature: cylindrical, oval, pellets with intact frustules, and minipellets (Urrere & Knauer 1981, Gowing & Silver 1985, González 1992a,b, González et al. 1994a, Buck & Newton 1995). Subsamples were taken and pellet concentration determined for each replicate, and the grand mean count was calculated. The maximum and minimum values for the two replicate samples were used to indicate the variance between traps.

4.2.2.2 Statistical analyses

Plankton were progressively integrated throughout the overlying water column to corresponding trap depths for the entire summer season. The data were transformed using the log (x+1) transformation to account for heterogeneity and to normalise the distributions in the data. Linear regressions were performed between the integrated abundance of plankton

(m^{-2}) in the overlying water column and the flux of faecal pellets (m^{-2} day^{-1}) to traps at each depth (e.g. the faecal pellet abundance at 40 m was regressed against the plankton abundance from 20-40, 10-40, 5-40, & 0-40 m). The correlation coefficient was used to determine the statistical significance of these relationships.

4.2.2.3 Microscopy

To obtain a representative cross-section of pellet types throughout the season, weekly samples were pooled for the examination of pellet morphology and ultrastructure.

Whole faecal pellets

Faecal pellets were isolated by micro-pipette and transferred to a droplet of 0.2 μm filtered sea-water. The water containing the pellet was mixed and the isolation repeated until the pellet was free from extraneous organic matter. Faecal pellets were then separated according to their morphology, and photographed under natural light at 400 x magnification using a Leitz Fluovert inverted microscope.

Various methods were used to minimise disruption of the faecal pellets during preparation for scanning electron microscopy (SEM). Oval and minipellets were pipetted onto 25 mm diameter nucleopore filters (5.0 μm pore size) and blotted to remove excess water. A subsample of an entire trap sample, that contained faecal pellets and other matter, was also pipetted directly onto a nucleopore filter to examine the complete array of pellets in the trap. Pellets containing whole diatom frustules were pipetted onto glass microscope slides that had been coated with polylysine (Marchant & Thomas 1983). Cylindrical pellets were pipetted into a nucleopore filter 'basket' that consisted of two layers of filter paper wedged between magnet rings. The filters and slides with attached samples were placed in petri dishes, gently washed with 10 % ethanol to remove traces of mercuric chloride, and fixed with osmium tetroxide vapour. They were then dehydrated through a graded ethanol series, followed by a concentrated solution of hexamethyl disilizane, and dried in a fume hood. The samples were subsequently mounted on carbon tabs with silver paint, and then on to stubs, sputter coated with gold, and examined by SEM.

Faecal pellet contents

Faecal pellets had been preserved in mercuric chloride, which reportedly inhibits bacterial ectoenzyme activity in seawater (Christian & Karl 1995). However, the extent to which mercuric chloride penetrates the faecal pellet is unknown. Pellets with membranes that masked the pellet contents were rinsed and pipetted into 0.2 μm filtered seawater and placed in an oven at 20 °C for 24 hours to allow for potential microbial stripping of the membrane (Turner 1984). In the event that microbial stripping did not occur I concurrently adapted a method used to clean diatom frustules and placed pellets in 50% hydrogen peroxide for 2-3 days (Battarbee 1986). All pellets were subsequently pipetted onto nucleopore filters and prepared for SEM (see above). It should be noted that the investigation of faecal pellet contents was used only to assist in determining the likely producers of pellets, and not as a determinant of species' diets.

4.3 Results

4.3.1 Plankton

This study examined the distribution and abundance of micro-pellets, and their relationship with the dominant plankton in the water column. Several copepod species (*Ctenocalanus citer, Drepanopus bispinosus, Stephos longipes* and *Euchaeta antarctica*), a larvacean, and echinoid larvae were not included in my analyses due to their low, or brief periods of abundance (see Chapter 3). In addition, pellets typical of the large, common, Antarctic copepod *Calanoides acutus* were not observed, the morphology of pellets produced by ctenophores is unknown (Reeve & Walter 1978), and pellets produced by heterotrophic nanoflagellates are reportedly too small (approximately 1 μm) to be detected by the methods used in this study (Elbrächter 1991). Therefore, these plankton were unlikely to have produced the pellets I observed and are not considered any further.

Small copepods were abundant throughout this study, especially in the upper 20 m of the water column, and showed extremely high spatial variability (SE from 1 to 100% of the mean) (Table 4.1). *Oncaea curvata* (Giesbrecht) was the dominant copepod reaching maximum concentrations

Table 4.1. Mean concentration of copepods (m^{-2}) at depth intervals from surface to 40 m. * signifies < 3 replicate samples where no standard error was calculated.

Species	Date	0-5 m Mean	SE	0-10 m Mean	SE	0-20 m Mean	SE	0-40 m Mean	SE
Oncaea curvata	16/12/97	0	*	94	32	232	91	325	*
	23/12/97	281	141	957	145	1257	52	1790	26
	28/12/97	212	153	991	283	2934	1046	3900	1314
	4/1/98	434	124	1967	275	4344	887	4443	1386
	11/1/98	592	217	1208	401	4739	690	4566	1750
	18/1/98	128	32	735	223	2505	226	3826	408
	25/1/98	10	10	108	51	789	256	2199	403
	1/2/98	64	10	74	31	680	157	1425	43
	8/2/98	79	20	44	9	1045	156	1637	590
	18/2/98	79	18	49	13	104	39	1755	271
	4/3/98	59	0	35	5	192	31	986	124
Paralabidocera antarctica	16/12/97	22	*	15	9	0	0	0	*
	23/12/97	79	30	84	18	5	5	20	5
	28/12/97	30	30	35	18	20	13	20	10
	4/1/98	69	30	64	18	69	25	64	36
	11/1/98	5	5	25	5	54	18	20	13
	18/1/98	30	15	84	13	182	21	138	13
	25/1/98	15	9	15	15	30	23	99	30
	1/2/98	30	15	44	30	84	35	99	44
	8/2/98	0	0	0	0	54	30	84	10
	18/2/98	5	5	5	5	5	5	10	5
	4/3/98	0	0	0	0	0	0	0	0
Oithona similis	16/12/97	0	*	0	0	10	10	15	*
	23/12/97	25	10	5	5	10	10	35	18
	28/12/97	5	5	5	5	10	5	35	18
	4/1/98	5	5	15	9	20	13	59	17
	11/1/98	25	5	35	18	123	75	123	101
	18/1/98	49	35	69	10	108	32	104	15
	25/1/98	20	5	44	15	49	26	49	20
	1/2/98	64	13	74	48	242	25	217	39
	8/2/98	35	5	39	13	222	112	237	87
	18/2/98	20	13	49	42	104	17	25	25
	4/3/98	0	0	64	13	148	30	375	49
Harpacticoids	16/12/97	0	*	0	0	0	0	0	*
	23/12/97	0	0	0	0	0	0	0	0
	28/12/97	0	0	0	0	0	0	0	0
	4/1/98	15	0	10	10	0	0	0	0
	11/1/98	0	0	0	0	5	5	0	0
	18/1/98	64	10	25	10	84	40	39	13
	25/1/98	25	10	44	15	20	10	10	10
	1/2/98	0	0	30	9	15	0	5	5
	8/2/98	0	0	5	5	20	10	0	0
	18/2/98	0	0	0	0	0	0	0	0
	4/3/98	0	0	0	0	0	0	0	0

in early January (Figure 4.1a, Table 4.1). This species increased in abundance during December to peak in January, but declined in February and March (Figure 4.1a). *Paralabidocera antarctica, Oithona similis* and harpacticoid copepods were in much lower abundance than *O. curvata* (averaging < 30 m^{-3}) (Figures 4.1a & b). *Paralabidocera antarctica* was present throughout December and January, but declined in February and was absent in March. In contrast, *O. similis* peaked during February and early March while harpacticoids exhibited a brief peak in mid January (Figure 4.1b).

Heterotrophic dinoflagellates (HDIN) were in low concentration throughout January, but increased to a peak concentration of 6.33×10^7 m^{-3} at ≤5 m in early February (Figure 4.1c). HDIN concentration was similarly high between 5 and 10 m at this time, while the concentration at ≥20 m depth increased later in the month. Mixotrophic *Ceratium* spp. dominated the HDIN taxa, however, *Gyrodinium* spp. and *Katodinium* spp. contributed to the HDIN concentration during late summer. *Amphidinium* spp. and *Protoperidinium* spp. were also present in low concentrations but reached maximum concentrations on 18 February of 8.92×10^6 m^{-3} between 10 and 20 m, and 4.54×10^6 m^{-3} between 20 and 40 m respectively. *Gymnodinium* spp. were also abundant, however, it is likely that most of the species I observed were autotrophic as the cells contained chloroplasts. Therefore, the abundance of this taxon was not included in the total HDIN abundance.

Ciliates comprised *Strombidium* spp., oligotrich genera, and tintinnids. The concentration of ciliates was much lower than that of HDIN but showed a similar temporal pattern of abundance. Ciliate concentration was low throughout January but increased in the upper 10 m in mid-February, with the peak concentration of of 3.96×10^7 m^{-3} at ≤5 m (Figure 4.1c). However, in contrast to that of HDIN, ciliate concentration at depths ≥20 m remained low throughout the season. Overall, the concentration of both HDIN and ciliates was highly variable (Figure 4.1c).

4.3.2 Faecal pellets

Cylindrical pellets were most abundant from December to January, with a peak flux of 1.20×10^4 pellets m^{-2} day^{1} observed at 40 m, but generally declined during February and March (Figure 4.2a). Oval pellets dominated

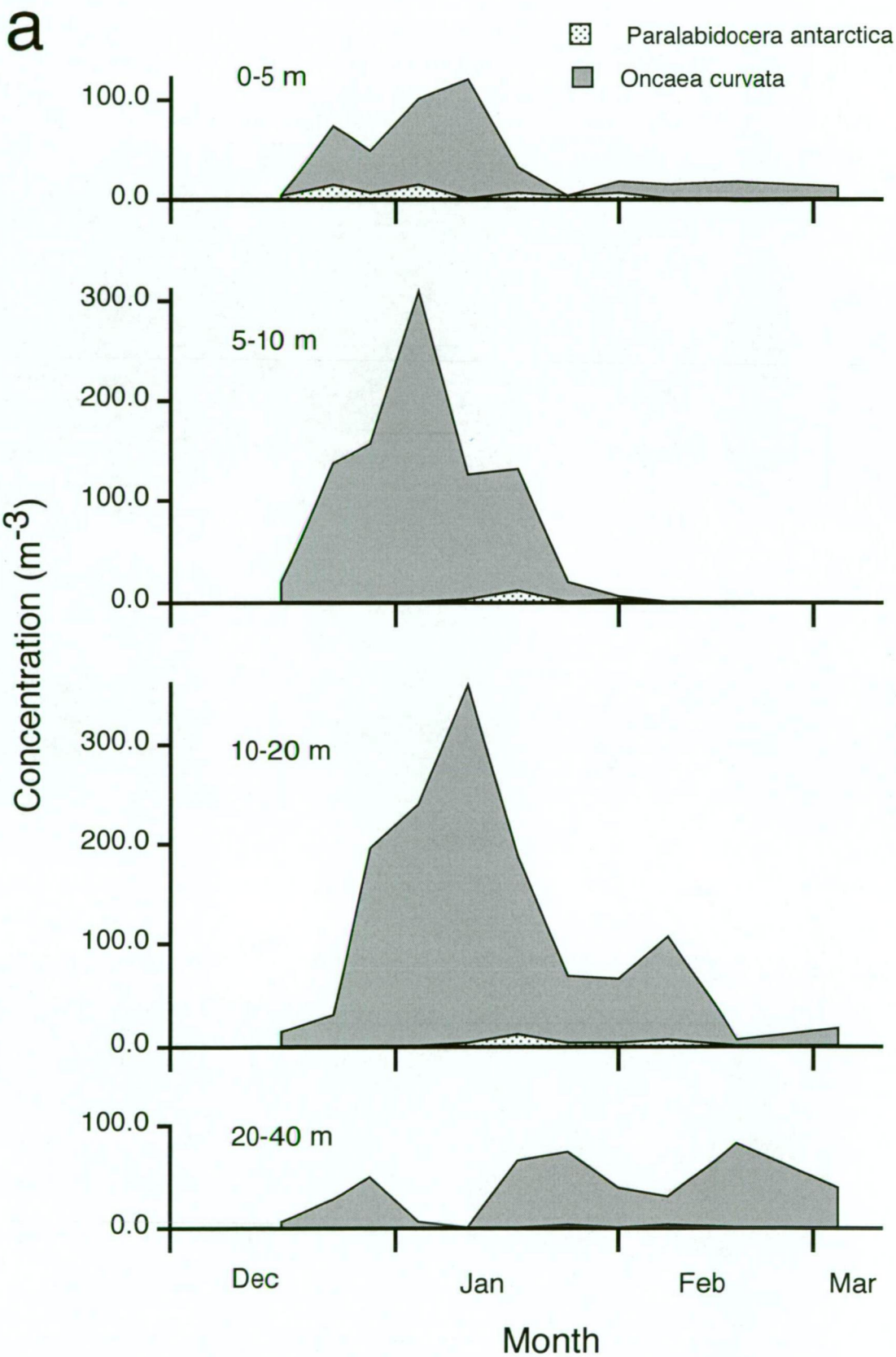


Figure 4.1a. The abundance of *Oncaea curvata* and *Paralabidocera antarctica* (error bars represent ± 1 SE) at 0-5 m, 5-10 m, 10-20 m, and 20-40 m in the water column.

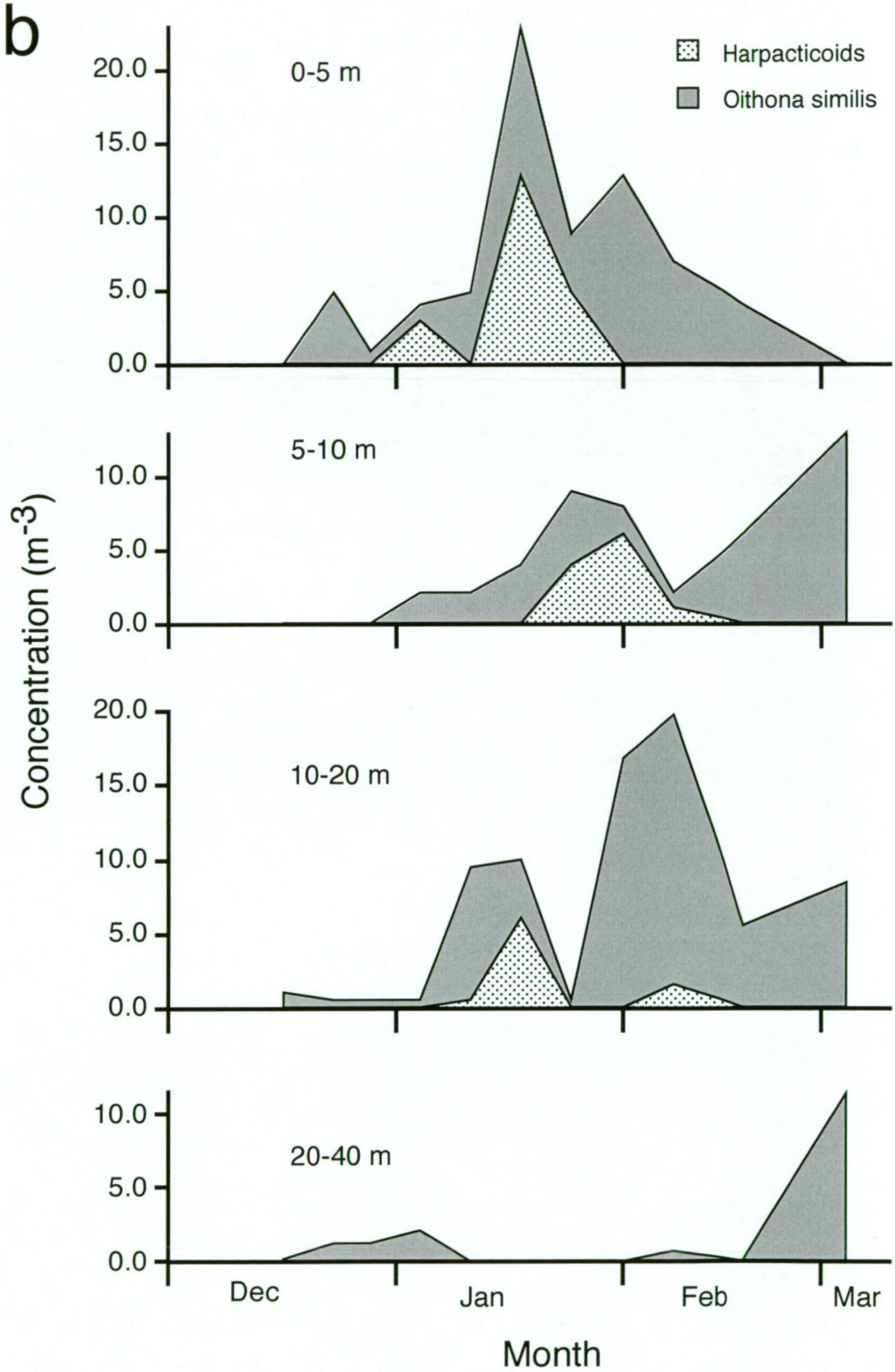


Figure 4.1b. The abundance of *Oithona similis* and harpacticoids (error bars represent ± 1 SE) at 0-5 m, 5-10 m, 10-20 m, and 20-40 m in the water column.

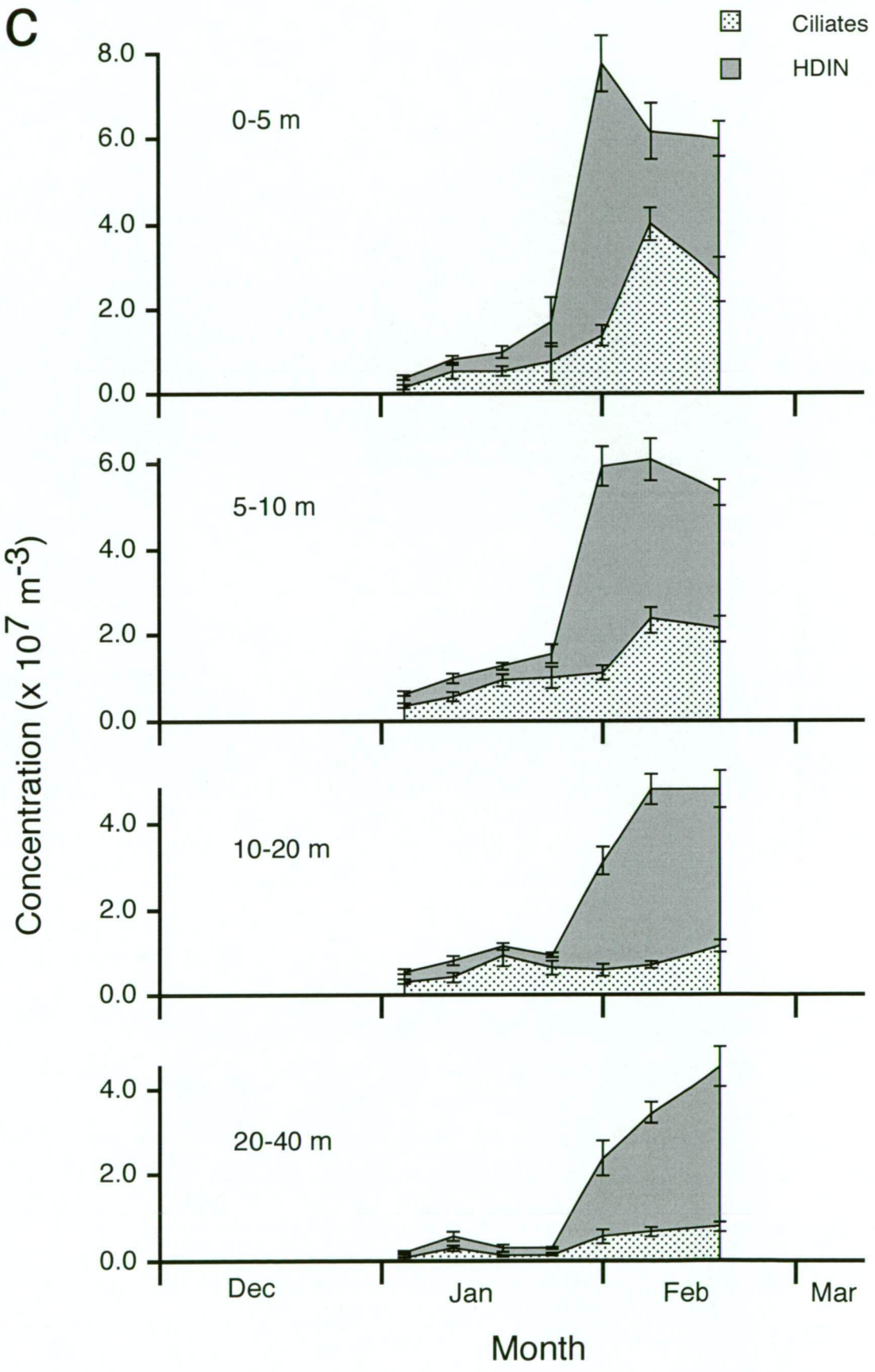


Figure 4.1c. The abundance of heterotrophic dinoflagellates (HDIN) and ciliates (error bars represent ± 1 SE) at 0-5 m, 5-10 m, 10-20 m, and 20-40 m in the water column.

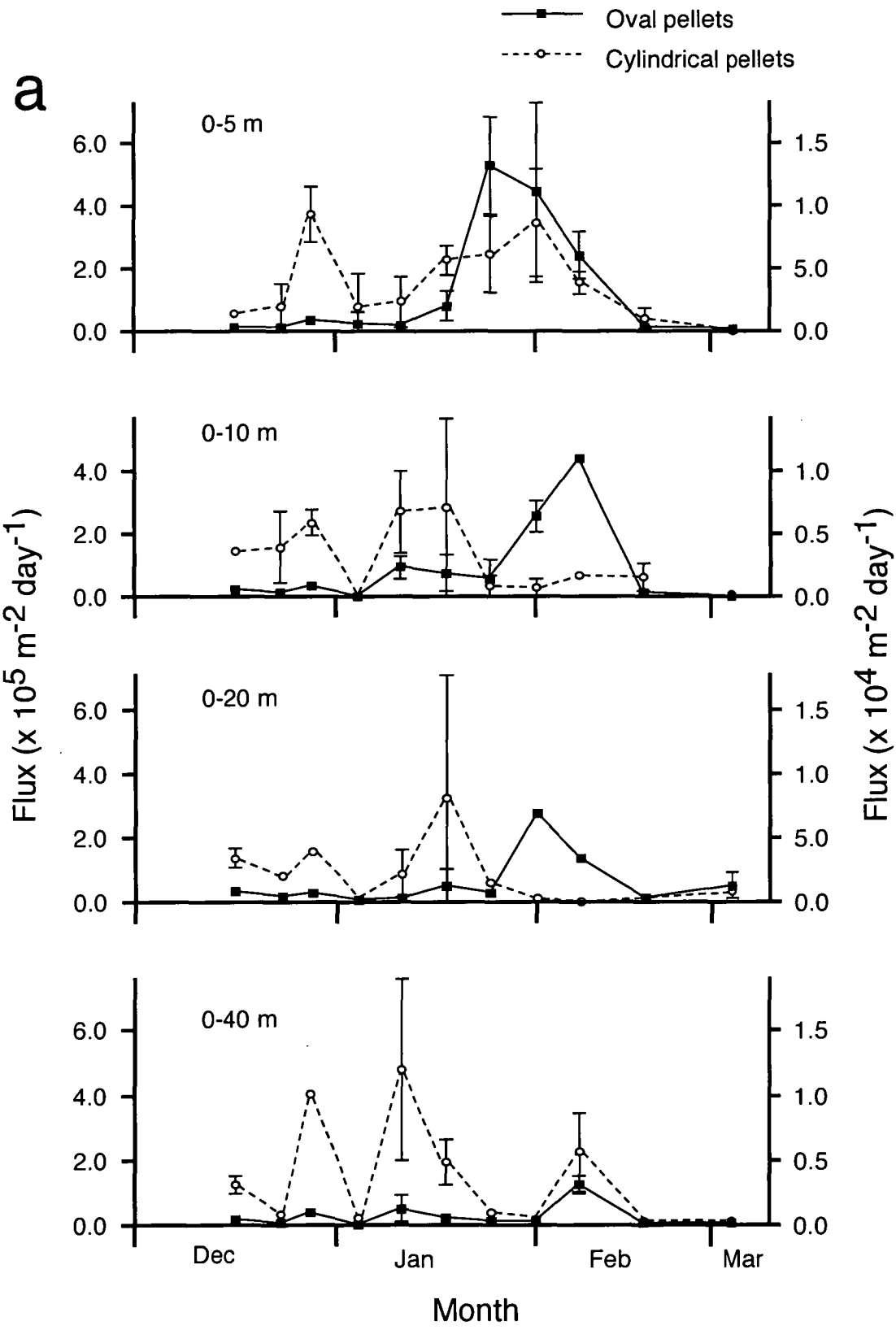


Figure 4.2a. Flux of oval (x 10^5 m^{-2} day^{-1}) and cylindrical pellets (x 10^4 m^{-2} day^{-1}) to 5, 10, 20 and 40 m depth. Error bars represent minimum and maximum values of the two replicate samples.

total pellet flux with a sedimentation peak of 5.24 x 10^5 pellets m^{-2} day^1 recorded at 5 m in late January. Sedimentation of these pellets persisted until late February in the upper 10 m of the water column. The flux of oval pellets to ≥20 m in the water column was low throughout this study.

Pellets containing only intact frustules sedimented throughout most of the season, predominantly in the upper water column, reaching 1.27 x 10^5 pellets m^{-2} day^1 at 10 m in mid-January and 1.15 x 10^5 pellets m^{-2} day^1 in early February. In contrast, minipellets showed only a brief period of sedimentation in the water column in mid February (Figure 4.2b). In general, the flux of minipellets to ≤20 m was low and highest flux was observed at 40 m (2.92 x 10^5 pellets m^{-2} day^1).

4.3.3 Plankton and faecal pellet correlations

While most plankton taxa did not correlate with the abundance of pellets in traps, significant correlations were observed between microzooplankton taxa and pellet types (Table 4.2).

Table 4.2. Significant correlations (all positive) between plankton species and pellet types. Cyl = Cylindrical, Mp = Minipellets, WC = Water column, P = Probability, n = number of samples

Organism	Pellet type	WC above trap depth	Trap Depth	r	n	P
Oithona similis	Cyl	0-5	5	0.656	11	0.02<p<0.05
	Mp	10-20	20	0.622	11	0.02<p<0.05
Harpacticoids	Mp	5-40	40	0.641	11	0.02<p<0.05
HDIN	Mp	0-10	10	0.754	7	0.02<p<0.05
	Mp	5-10	10	0.798	7	0.02<p<0.05
	Mp	0-20	20	0.920	7	0.002<p<0.005
	Mp	5-20	20	0.913	7	0.002<p<0.005
	Mp	10-20	20	0.890	7	0.02<p<0.05
Ciliates	Mp	0-10	10	0.876	7	0.005<p<0.01
	Mp	5-10	10	0.827	7	0.02<p<0.05

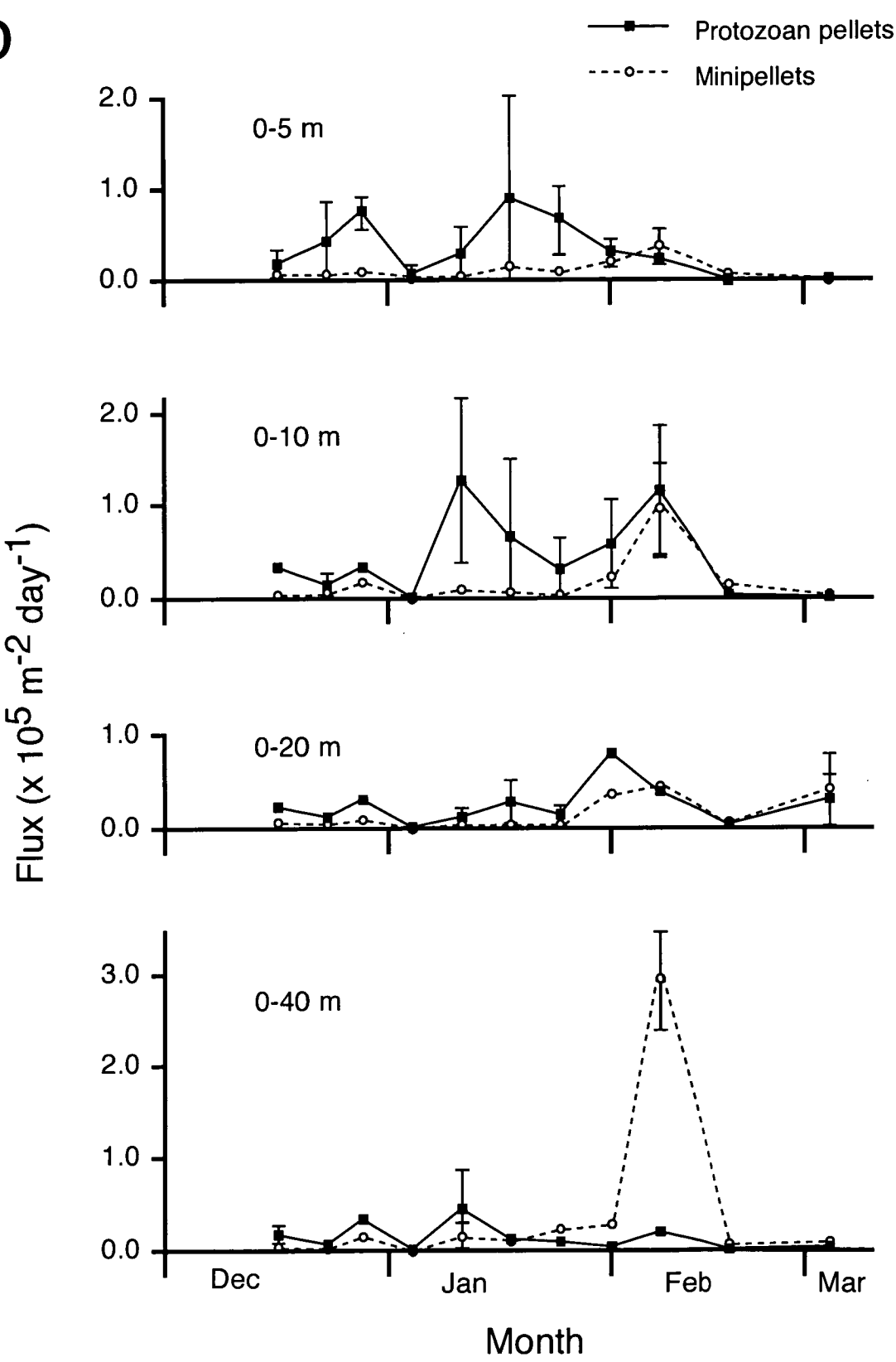


Figure 4.2b. Flux of pellets with intact frustules (protozoan) pellets and minipellets to 5, 10, 20 and 40 m depth. Error bars represent minimum and maximum values of the two replicate samples.

The abundance of *Oncaea curvata* and *Paralabidocera antarctica* from early to mid summer (December–January) coincided with the flux of cylindrical faecal pellets in the water column. In particular, the occurrence of pellets at 40 m resembled the abundance of these species of plankton between 10 and 20 m (Figures 4.1a & 4.2a). No significant correlations were observed between the abundance of these species and that of cylindrical pellets. However, the abundance of *P. antarctica* between 5 and 10 m and the flux of cylindrical pellets to 10 m showed a relationship that approached significance ($0.05<p<0.10$).

The abundance of *Oithona similis* and harpacticoids in late January and February coincided with the flux of oval pellets in the water column (Figures 4.1b & 4.2a), and near-significant correlations were observed between the two ($0.05<p<0.10$). *Oithona similis* and harpacticoids at ≥20 m significantly correlated with the flux of minipellets to 20 and 40 m respectively (Table 4.2), and the abundance of *O. similis* in the upper 5 m showed a near-significant correlation with the flux of minipellets to 5 m ($0.05<p<0.10$). Furthermore, the abundance of *O. similis* showed a consistent, but not significant, negative relationship ($-0.989<slope<-0.831$) with the abundance of cylindrical pellets at depth intervals throughout the water column (data not shown), except at ≤5 m where I observed a significant positive correlation between *O. similis* and cylindrical pellets.

Heterotrophic dinoflagellates were most abundant from mid to late summer, and pellets with intact frustules were abundant in traps throughout the season (Figures 4.1c & 4.2b). While both the concentration of organisms and the flux of pellets were greatest in the upper 10 m of the water column, they were not significantly correlated ($p>0.2$). In contrast, the concentration of HDIN at depth intervals ≤20 m significantly correlated with the flux of minipellets to traps at 10 and 20 m depths.

The abundance of ciliates in the upper 10 m of the water column in mid February coincided with an abundance of minipellets, and a significant correlation was observed between the two at ≤10 m.

4.3.4 Faecal pellet morphology and ultrastructure

Nine different faecal pellet types were discriminated on the basis of their morphology and ultrastructure (Table 4.3).

4.3.4.1 Cylindrical pellets

Cylindrical pellets largely contained diatom fragments with no interstitial connective material but some whole frustules of *Thalassiosira* sp., *Nitzschia stellata* and *Nitzschia prolongatoides* were observed (Table 4.3, Figures 4.3a-c). I also occasionally observed microbial degradation of the bounding membrane surrounding these pellets (Figure 4.3d). Cylindrical pellets were poorly retained on standard nucleopore filters and polylysine coated microscope slides, and had to be contained in a filter 'basket' during preparation for SEM.

4.3.4.2 Oval pellets

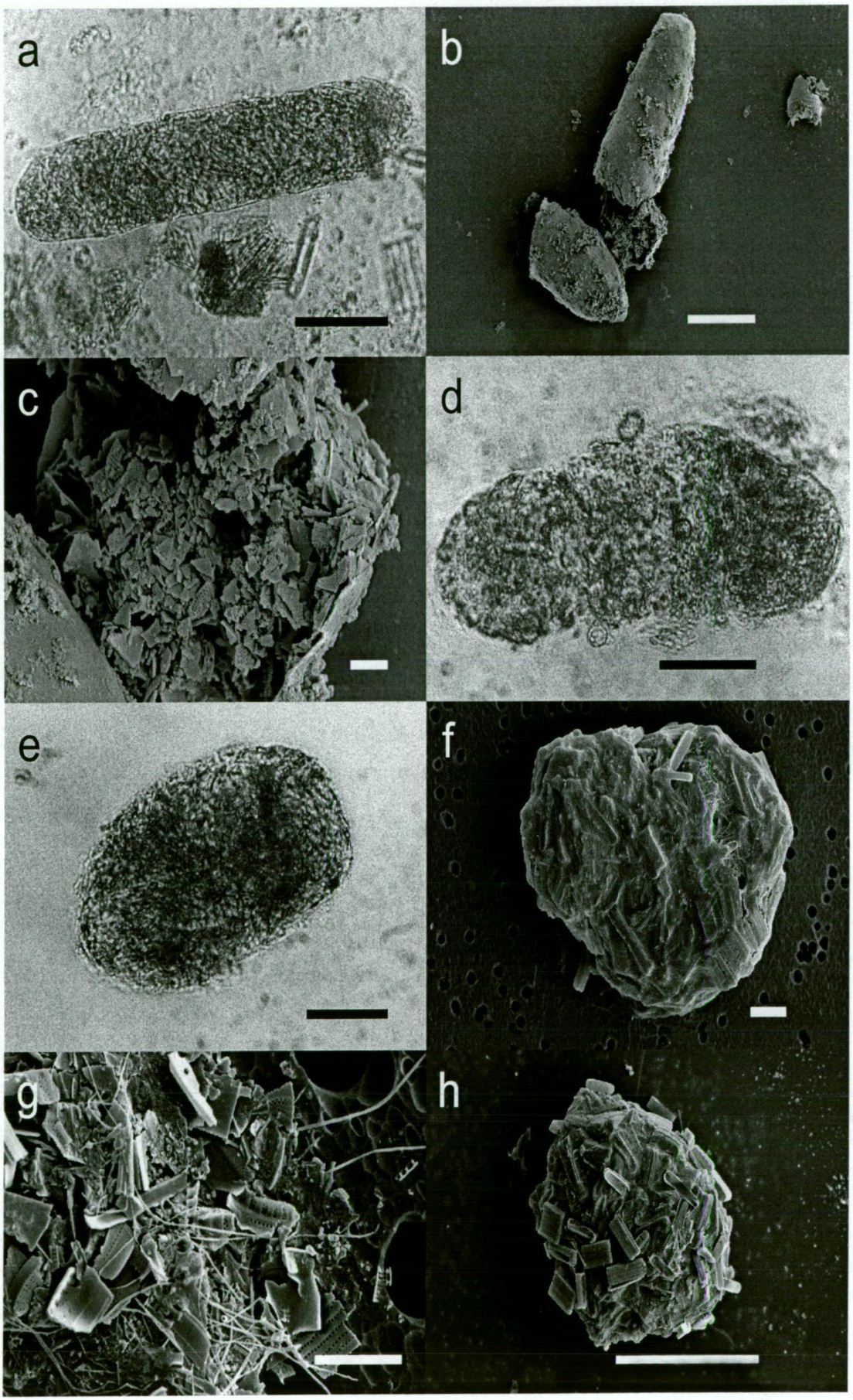
Oval faecal pellets were densely packed, membrane bound and varied considerably in size (Table 4.3, Figures 4.3e & f). These pellets largely contained fragmented frustules of *Fragilariopsis curta* and *Fragilariopsis cylindrus* (Figure 4.3g). However, oval pellets also contained filamentous threads and organic matter in the interstitial spaces between frustules (Figure 4.3g), and occasional whole diatom frustules, dinoflagellate cysts, and chryosphyte statocysts. Whole frustules were also observed adhered to the outer surface of the pellet (Figure 4.3h). The pellets were resilient during handling and preparation in the laboratory, and the membrane remained largely intact after microbial stripping.

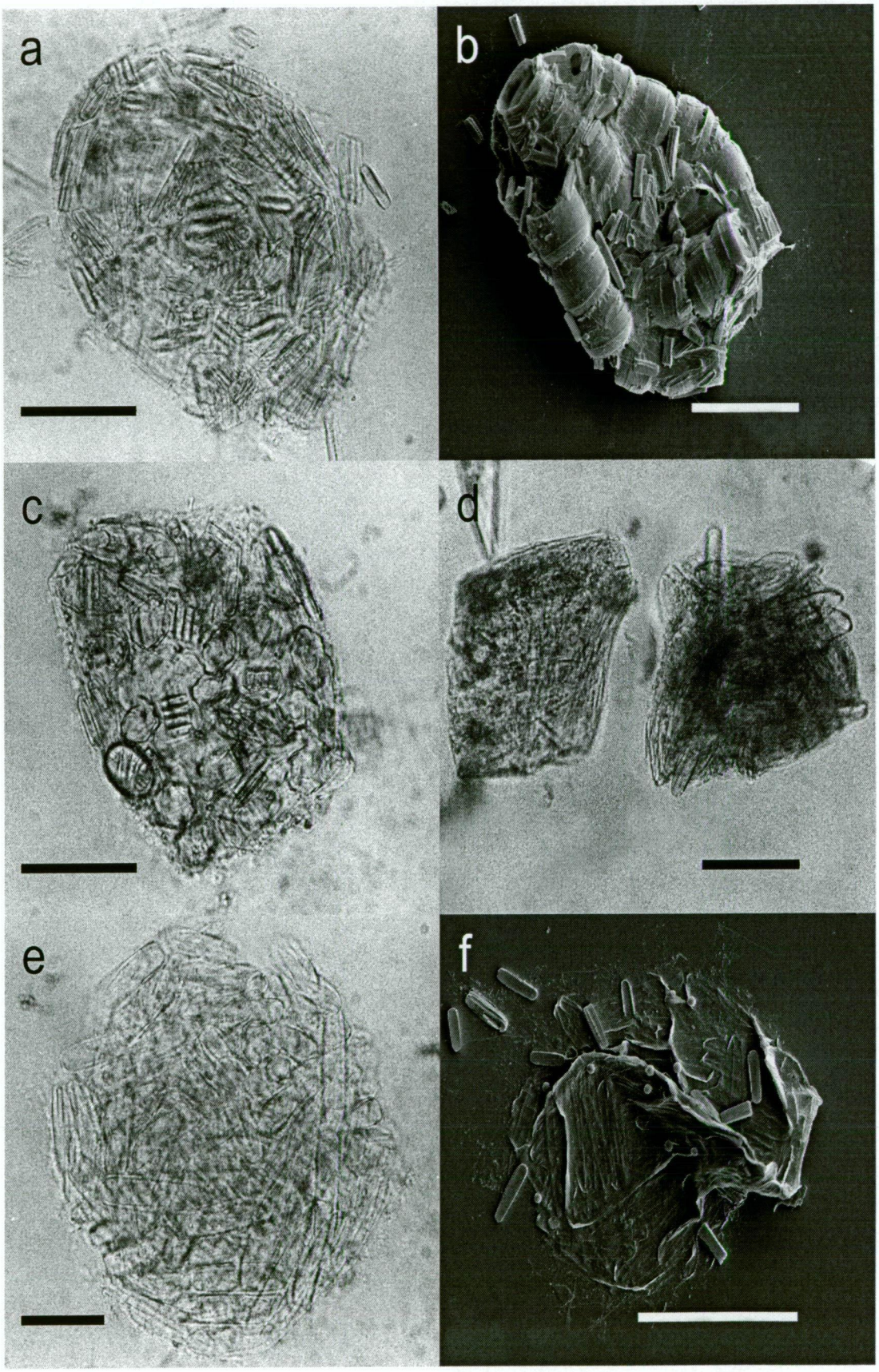
4.3.4.3 Faecal pellets with intact frustules

Three types of membrane-bound faecal pellets containing intact, empty frustules were evident by light microscopy (LM) (Table 4.3, Figure 4.4a-e). Oval pellets contained either one species of diatom (often chain-forming) (Figures 4.4a &b), or a variety of intact pennate and centric diatom frustules (Figure 4.4c). Irregular and round pellets contained frustules of a single pennate diatom species (Table 4.3, Figures 4.4d & e). All pellets appeared semi-transparent when viewed by LM, and some details of the frustules within the pellets were evident through the bounding membrane.

Table 4.3. The types, sizes, contents and proposed origin of faecal pellets in sediment traps throughout the upper 40 m of the water column during summer in Ellis Fjord. Where pellet sizes were consistent the dimensions were averaged. Pellets varying greatly in size are presented as ranges. ∅ represents diameter, MB indicates membrane bound, DF indicates fragmented diatom frustules, WD indicates whole diatom frustules, + or - CM indicates with or without interstitial connective material

Pellet type	Average or range in size (μm)	Contents	Proposed origin
Cylindrical	250 x 73	MB, DF, -CM	*O. curvata* & *P. antarctica*
Oval	80 x 60 to 190 x 155	MB, WD & DF, cysts, +CM	*O. similis* & harpacticoids
Intact frustules			
Oval	150 x 110	MB, WD of single or multi-species -CM	Athecate dinoflagellates
Irregular	130 x 120	MB, WD of single species, -CM	Phagotrophic dinoflagellates
Round	150-250 ∅	MB, WD of single species, -CM	Pallium-feeding dinoflagellates
Minipellets			
Oval	25 x 18 to 60 x 35	±MB, DF<10 μm, detritus & crushed material	Dinoflagellates & ciliates
Spherical	60-80 ∅	MB, DF, WD>20 μm	Copepod nauplii
Semi-transparent	30 ∅	MB, WD	Dinoflagellates
False	50 ∅	Partially MB, DF	By-product of coprophagy


a
b
c
d
e
f
g
h


a
b
c
d
e
f

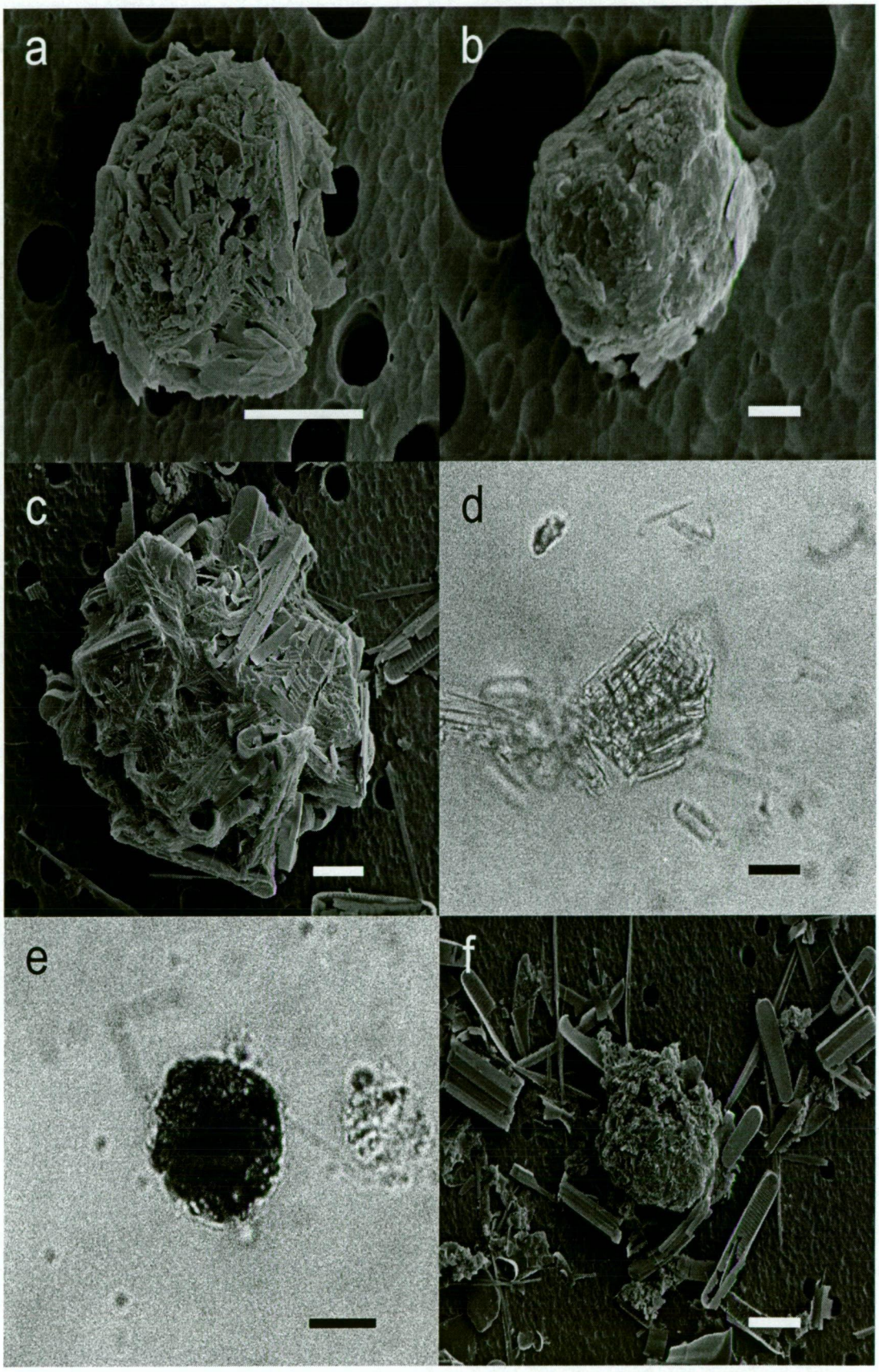
In addition, the membrane frequently ruptured during handling and the integrity of the pellet contents was not retained (Figure 4.4f).

4.3.4.4 Minipellets

Four types of minipellets were evident. It was not possible to determine whether interstitial connective material was present in minipellets. Oval and spherical minipellets appeared consolidated: pellets were opaque under LM and their contents were densely packed. Oval minipellets were observed both with and without a bounding membrane and contained detritus, crushed material and fragments of small (< 10 μm long) diatoms (Table 4.3, Figure 4.5a & b). Spherical minipellets were membrane-bound and contained diatom fragments and whole frustules > 20 μm (Table 4.3, Figure 4.5c). Semi-transparent minipellets, discriminated using LM, were small, oval to irregular in shape, membrane-bound, and contained intact pennate diatom frustules (Table 4.3, Figure 4.5d). These pellets were not as common as consolidated minipellets under LM (Figure 5e). Observation of a complete trap sample by SEM also showed minipellets that were partially membrane-bound (Table 4.3, Figure 4.5f) and resembled the end of a cylindrical pellet (see Figure 4.3d).

4.4 Discussion

Micro-copepods and protozoa are major contributors to heterotrophic biomass in the oceans (Lessard 1991, Metz 1998, MZC2 2001). These microzooplankton graze much of the primary production in upper waters and contribute to particle aggregation via the production of faecal pellets (Buck et al. 1990, Garrison 1991, Verity & Vernet 1992, Metz 1998). It has been reported that particles > 100 μm contribute most of the vertical carbon flux in the oceans (e.g. Fowler & Knauer 1986, Williams et al. 1989, Fortier et al. 1994). However, surprisingly little work has been done to investigate species-specific differences among microzooplankton pellets, nor their persistence in the water column and contribution to this flux. Here I examine the distribution, abundance and ultrastructure of each faecal pellet type observed in sediment traps from Ellis Fjord and determine their likely producers and fate.


a
b
c
d
e
f

While significant correlations were observed between the abundance of plankton taxa and the flux of individual pellet types, I also observed near-significant ($0.05<p<0.10$) relationships where the magnitude of the slope was high and consistently positive or negative with depth. This indicated a consistent relationship between individual plankton taxa and pellet flux. These near-significant correlations suggest that the linkage between plankton and the vertical flux of their faecal pellets was affected by the mediation of pellet flux by trophic processes (e.g. coprophagy and microbial degradation), and the spatial and temporal variability in plankton and pellet abundance. The vertical distribution of copepods is reportedly highly variable and no consistent pattern of diel vertical migration has been observed in Ellis Fjord (Kirkwood 1993). Swimmers can also confound relationships between plankton and pellet flux by voiding their guts upon entering poisoned traps (Harbison & Gilmer 1986). However, few swimmers were observed in trap material and *in vitro* studies of copepods (the most abundant swimmers) showed that animals did not void their guts upon contact with mercuric chloride and brine solution, nor did brine cause any herniation of copepod guts (see Chapter 2).

4.4.1 Cylindrical pellets

The abundance of *O. curvata* and *P. antarctica* in early summer coincided with the flux of cylindrical pellets in the water column. *Paralabidocera antarctica* reportedly produces cylindrical pellets around 350–450 μm long (Tanimura et al. 1984). The morphology of *O. curvata* pellets is unknown, but cylindrical pellets, ranging from 70–260 μm in length, were produced by a temperate *Oncaea* sp. (Turner unpubl. data). There were no significant correlations between the abundance of these copepods and cylindrical pellets, although *P. antarctica* showed a near-significant relationship with these pellets at ≤10 m ($0.05<p<0.10$). The greatest flux of cylindrical pellets was observed at 40 m, and resembled the abundance of *O. curvata* and *P. antarctica* between 10 and 20 m, indicating these pellets persisted throughout the water column and contributed to vertical flux.

A negative relationship ($0.05<p<0.10$) between the abundance of *O. similis* and the flux of cylindrical pellets at all depths ≥5 m was observed, supporting the findings of González & Smetacek (1994) that this copepod

engages in coprophagy. Coprophagy in the water column can reportedly decrease the abundance of some pellets by up to 75% (González & Smetacek 1994) and while *O. curvata* dominated the copepod abundance, cylindrical pellets were the least abundant pellet-type collected in sediment traps. Cylindrical copepod pellets can contain undigested chlorophyll *a* (Bathmann & Liebezeit 1986, Nelson 1989), and it has been suggested they may provide a nutrient source for other plankton (Smetacek 1980, González et al. 1994a). However, similar to Bathmann et al. (1987), I found that cylindrical pellets were easily damaged in the laboratory and degraded during preparation for SEM. Therefore, microbial and physical degradation could also have contributed to the overall low abundance of cylindrical pellets collected in sediment traps, particularly when heterotrophy predominated in the latter half of the season (see Chapter 3). The significant positive correlation between the abundance of *O. similis* and the flux of cylindrical pellets at ≤5 m suggests that coprophagy is facultative: high concentrations of protists, such as the ice-algal mat, may provide ample food and reduce coprophagous feeding.

Cylindrical pellets could be easily identified by their overall morphology using LM. The size (> 200 μm), shape (cylindrical) and optical density (opaque) were characteristic of 'typical' copepod pellets (Marshall & Orr 1955, Honjo & Roman 1978, Martens 1978). Furthermore, investigation of pellet ultrastructure using SEM showed that pellets predominantly contained compacted fragments of diatoms and occasional whole frustules reflecting raptorial feeding (González et al. 1994a), and showed little distortion of the bounding membrane.

4.4.2 Oval pellets

Oithona similis was abundant throughout the season and reportedly produces small oval pellets that can vary in size, ranging from 20–120 μm, even in the presence of a constant food source (Martens 1978, González et al. 1994a). The abundance of *O. similis* did not significantly correlate with that of oval pellets. However, relationships ($0.05<p<0.10$) were observed at ≤20 m in the water column where *O. similis* was most abundant suggesting that these copepods produced oval pellets (Table 4.3). To my knowledge, the shape of harpacticoid pellets has not been described. However, similar to *O. similis*,

harpacticoids may produce oval pellets, as a weak correlation ($0.05<p<0.10$) was observed between the abundance of harpacticoids and oval pellet flux.

Oithona similis, harpacticoids and oval pellets were abundant in near-surface waters. While the maximum abundance of *O. similis* and harpacticoids occurred in mid to late summer, their concentrations were around 10 times less than that of *O. curvata*. However, oval pellets were up to 50 times more abundant than cylindrical pellets. Similar to González (1992a), my laboratory observations suggest oval pellets were resistant to mechanical stress and microbial breakdown, and the high abundance of these pellets in surface waters relative to the concentration of their planktonic producers suggests that they may be persistent. Cadée et al. (1992) reported that oval pellets (150–350 μm long) had relatively high sinking rates (80–250 m day $^{-1}$). In contrast, my results showing high pellet abundance in surface waters and low flux to depth indicated low sinking rates and eventual pellet breakdown. Many reasons have been proposed why pellet flux is retarded in the water column (Bathmann et al. 1987, Noji et al. 1991, González et al. 1994b) and we previously suggested that the low flux of oval pellets resulted from coprophagy (Beaumont et al. 2001). However, statistical analyses did not support this as there were no substantial negative relationships between the abundance of copepods and oval pellets.

Oval pellets produced by *Oithona similis* and harpacticoids, while relatively small, contained highly compacted diatom fragments as well as intact algal frustules typical of pellets produced by cyclopoid copepods (Adrian 1987). However, similar to pellet contents described from a temperate harpacticoid species (Dahms 1993), these pellets also contained non-diatomaceous and other organic material that may contribute to their reduced sinking rates (Bienfang 1980, Hansen et al. 1996, Feinberg & Dam 1998).

4.4.3 Pellets with intact frustules

Pellets containing intact frustules were the second most abundant type of faecal pellet. These pellets resembled descriptions of pellets produced by protozoa (Stoecker 1984, Buck et al. 1990, Buck & Newton 1995) however, the concentration of protozoa did not significantly correlate with the abundance of these pellets. The lack of correlation may be due to a number of factors.

Firstly, this may have been an artefact of my sampling methods. I did not sample protozoa in the ice and they may have contributed substantially to the abundance of pellets in the water column. Furthermore, obtaining weekly 2 L samples may not have encompassed the high spatial and temporal variability of the protozoan community. Fixation with Lugol's iodine may also have led to the loss of some organisms sampled (see Chapter 3, 3.2.1 Sampling). In addition, the accurate determination of the trophic status of dinoflagellate species is problematic, and estimates of protozoan abundance exhibited high variance due to their rare occurrence in microscope counts. Second, production of pellets may be variable due to the large amount of nutrition likely to be obtained from a single feeding event. Third, the variable abundance of these pellets may be due to high rates of degradation and disintegration of some pellets (see below).

Protozoan pellets were most abundant in the upper 10 m of the water column. They were relatively large (averaging 150 μm in diameter) but contained intact diatom frustules, greatly reducing the density of siliceous material in the pellet (see below). A large pellet volume relative to specific weight reportedly retards pellet flux (Madin 1982), and the low abundance of these pellets I observed at depth indicates that these large protozoan pellets contributed little to vertical flux. This agrees with the finding of González (1992b), but contrasts with that of Gowing et al. (2001) who reported large protozoan pellets sedimenting to depth. The morphology of ovoid pellets reported by Gowing et al. (2001) suggests they may not be of protozoan origin. However, differences in feeding mechanisms among protozoan genera could affect pellet morphology and production, and consequently the abundance and persistence of pellets in the water column.

Our observations of the morphology and ultrastructure of pellets containing intact frustules using LM and SEM showed three distinct morphological types. Oval pellets appeared the most compact and robust of the pellet types, and were frequently the most abundant protozoan pellet observed in sediment traps. These pellets were membrane-bound containing mixed diatoms or single diatom species and such pellets have previously been attributed to protozoans (Nöthig & von Bodungen 1989, González 1992b). These oval pellets most resembled those produced by an athecate dinoflagellate in Antarctic sea-ice and underlying waters (Buck et al. 1990).

Pasternak et al. (2000) recently reported that small larvaceans also produce oval pellets and these pellets contained only whole diatom frustules (A. Pasternak pers. comm.). However, larvaceans were not abundant in my study.

Irregular pellets were similar to those previously recorded in coastal waters (Nöthig & von Bodungen 1989, González 1992b, Buck & Newton 1995, Saito et al. 1998), and are reportedly produced by heterotrophic dinoflagellates that directly engulf their prey (Elbrächter 1991, González 1992b, Buck & Newton 1995). *Gyrodinium* spp. have been observed ingesting diatom chains and reportedly produce pellets containing monospecific diatom frustules similar to the irregular pellets I observed (Nöthig and von Bodungen 1989, González 1992b, Buck & Newton 1995). Therefore, the *Gyrodinium* spp. that were abundant in this study are likely to have produced most of these irregular pellets (Table 4.3). However, other dinoflagellates that engulf their prey, such as heterotrophic *Gymnodinium* spp. could also have contributed to their production.

To my knowledge, the large, round, semi-transparent pellets I observed have only been reported in a single study in coastal waters off California, USA (Urrere & Knauer 1981). Their large size and contents suggest they may be the pallium of extracellular feeding dinoflagellates that engulf and digest their prey within a feeding veil (termed a pallium), enabling them to feed upon prey items larger than their own body size (Gaines & Taylor 1984, Jacobson & Anderson 1986, Schnepf & Elbrächter 1992). The pallium reportedly retracts after feeding and presumably the remains are dispersed (Elbrächter 1991). Therefore, I suggest these pellets may result from dislodgement of the pallium due to interruption while feeding, or if the pallium is renewed by the organism, and the occurrence of these pellets is likely to be rare. Members of the genus *Protoperidinium* spp. are known to be pallium-feeders (Gaines & Taylor 1984, Hansen & Calado 1999), and the *Protoperidinium* spp. I observed may have produced these pellets. Furthermore, I observed an unidentified HDIN with an apparent pallium that contained empty, compacted diatom frustules.

4.4.4 Minipellets

Minipellets were most abundant in the latter half of the season when HDIN and ciliates reached maximum concentration. These pellets are reportedly produced by a range of protozoa such as HDIN, ciliates, radiolarians and heterotrophic flagellates (Stoecker 1984, Gowing & Silver 1985, Elbrächter 1991, Silver & Gowing 1991). Radiolarians were not recorded in this study, and the methods I used would not have detected faeces produced by heterotrophic flagellates (see above). The abundance of HDIN, at depth intervals between 0 and 20 m, significantly correlated with the flux of minipellets to 10 and 20 m, while the abundance of ciliates at ≤10 m significantly correlated with minipellet flux to 10 m. However, neither the abundance of HDIN nor ciliates significantly correlated with the highest abundance of minipellets recorded at 40 m.

Minipellets, due to their size and morphology, are presumed to have low sinking rates and would not be expected to sink to depth (Stoecker 1984, Gowing & Silver 1985, Elbrächter 1991). However, similar to my findings, they have often been recorded in high abundance in deep waters (Gowing & Silver 1985, Nöthig & von Bodungen 1989, González et al. 1994b). The morphology of minipellets was difficult to discern using LM as they were small and generally opaque. Observations of their morphology using SEM showed there were four types of minipellets.

Oval minipellets, containing detritus and small diatom fragments, were observed both with and without a bounding membrane and resembled pellets produced by both dinoflagellates and ciliates (Stoecker 1984, Buck et al. 1990, Elbrächter 1991).

Small, spherical minipellets were similar in structure and contents to the dense oval pellets produced by *O. similis* and harpacticoids (see 4.4.2 Oval pellets), and the size of these minipellets was similar to those produced by copepod nauplii in the laboratory (Pasternak et al. 2000). Copepod nauplii were only occasionally observed in net haul samples but the mesh size of my net (100 μm) probably under-sampled these organisms (see Pasternak et al. 2000). Thus, these spherical minipellets were probably produced by copepod nauplii.

Semi-transparent minipellets containing whole diatom frustules resembled the irregular pellets that I attributed to phagotrophic dinoflagellates (see above). These pellets have previously been recorded from Antarctic waters across a broad size range (5 - 120 μm) (González 1992b), their size reportedly being determined by the quantity and species composition of available food (Elbrächter 1991). Therefore, dinoflagellates appear capable of producing faecal pellets of variable size, from minipellets to pellets comparable in size, or larger than, those produced by small copepods.

The fourth type of minipellet I observed resembled the degraded end of a cylindrical pellet and I termed these 'false minipellets'. Faecal pellets reportedly degrade as they sink (Honjo & Roman 1978, Martens & Krause 1990), and coprophagy and ablation in the water column fragments pellets and aids their degradation by microbes (Honjo & Roman 1978, Lampitt et al. 1990, Noji et al. 1991). Statistical analyses showed significant correlations between the abundances of *O. similis* and harpacticoids and minipellet flux to 20 and 40 m respectively. Therefore, coprophagy of cylindrical pellets by *O. similis* and harpacticoids may have contributed to the production of false minipellets. Furthermore, the lack of correlation between protozoan abundance and minipellet flux to depth suggests that false minipellets comprised the majority of minipellets in sediment traps at 40 m. Therefore, production of false minipellets due to coprophagy and degradation may assist in explaining the abundance of minipellets in deep waters reported in previous studies (see above).

Most studies investigating particle flux have used only LM to examine faecal pellet morphology and abundance. While LM is necessary for quantitative analysis of sediment trap material, it limits the ability to resolve detailed structure and morphology of pellets. Under the light microscope, I observed copepod pellets that appeared free of external matter. However, when viewed using SEM, whole diatoms were observed adhered to the outer surface of the pellet that may be confused with pellet contents under the light microscope. Furthermore, previous studies have reported difficulties in distinguishing faecal pellets from protozoa when viewed by LM (Nöthig & von Bodungen 1989, Gowing et al. 2001). Therefore, I propose that the classification of faecal pellets using LM be validated using SEM.

4.4.5 Contribution by copepods and protozoa to vertical flux

It is generally believed that heterotrophic grazing facilitates the export of primary production, and biogenic particles greater than 100 μm are primarily responsible for vertical carbon flux in the oceans (e.g. Fowler & Knauer 1986, Williams et al. 1989, Fortier et al. 1994). However, in northern hemisphere waters, the retention of a variety of pellet types (large cylindrical, oval, protozoan, minipellets) has been observed (Smetacek 1980, Hofmann et al. 1981, Martens & Krause 1990, Wassmann et al. 1994, Viitasalo et al. 1999, Pasternak et al. 2000). In Antarctic waters there has been little consensus on the fate of faecal pellets. Large cylindrical pellets have been reported to be retained in upper waters, but in conjunction with oval pellets they can also contribute to vertical flux (Bathmann et al. 1991, Cadée et al. 1992, González 1992a, Suzuki et al. 2001). Furthermore, it has been proposed that protozoan pellets can contribute substantially to carbon export (Nöthig & von Bodungen 1989, Buck et al. 1990, Bathmann et al. 1991, González 1992a, Gowing et al. 2001). I found that small cylindrical pellets from *O. curvata* and *P. antarctica* can also sediment to depth. However, oval pellets produced by *O. similis* and small harpacticoid copepods, and protozoan pellets were retained in upper waters irrespective of their diverse range in size, shape and ultrastructure. My results indicate that the contribution by microzooplankton to vertical carbon flux is largely determined by the species-specific origin of the pellets that defines their structure and morphology, rather than pellet size. Consequently, changes in community structure over fine spatial and temporal scales and due to long-term global climate change will influence the role of the plankton community in vertical carbon flux, with ramifications for the accumulation of greenhouse gases in the atmosphere.

Chapter 5

The contribution by the protistan community to direct vertical flux

5.1 Introduction

As primary producers, autotrophic protists are instrumental in trapping carbon dioxide derived from the atmosphere, thereby providing the first step in the sequestration of atmospheric carbon in the oceans (Longhurst & Harrison 1989, Siegenthaler & Sarmiento 1993, Azam 1998, Falkowski et al. 2000). Heterotrophic protists also play an important role in the remineralisation of carbon and nutrients in the world's oceans, particularly nanoplanktonic heterotrophs that form part of the microbial loop (e.g. Sherr & Sherr 1988, Banse 1992, Azam 1998). The contribution by microplanktonic heterotrophs to carbon flux has received less attention, although it has recently been suggested that their grazing, and subsequent production of faecal pellets, may play a considerable role (see Chapters 4 & 6). In Antarctic waters, many studies have investigated protistan production, species composition and succession in the water column (e.g. Garrison et al. 1988, Jacques & Panouse 1991, Nöthig et al. 1991), and several studies have investigated the composition of protists from sediment traps (e.g. Sasaki & Hoshiai 1986, von Bodungen et al. 1986, Leventer 1991). However, the relationship between the water column assemblage and the direct flux of protistan taxa, as compared to that mediated by grazers, has received little attention (Karl et al. 1991, Wassmann 1998). Consequently, little is known about the processes that regulate the contribution by individual taxa to vertical flux, though recognition of the role of aggregates as hot-spots of microbial production in the water column suggests that aggregation may promote the flux of a variety of protistan taxa (Silver et al. 1978, Silver & Gowing 1991, Marchant et al. 1996, Azam 1998).

The complexity of biological and physical processes in the open ocean hinders detailed investigations of protistan flux over large time periods.

Consequently, there is a need for studies of plankton ecology and biogeochemical processes in simplified macrocosms, e.g. enclosed or semi-enclosed waters (Wassmann 1998, Trull et al. 2001). Ellis Fjord provides an ideal macrocosm in which protistan dynamics can be examined at fine spatial and temporal scales (see Chapter 1). It supports a protistan community representative of that in the Southern Ocean (see Chapter 3), which contributes to particulate flux (see Chapters 2 & 4). This chapter investigates the relationship between the species composition of the suspended protistan assemblage and flux to depth, and the influence of community succession on the regulation of protistan vertical flux at weekly intervals throughout an Antarctic summer.

5.2 Methods

The data presented here for the protistan assemblage in the water column are based on concentrations presented in Chapter 3. To enable comparisons with the protistan assemblage from sediment traps, the laboratory methods are reiterated, and the concentrations obtained from discrete depths in Chapter 3 are integrated between depth intervals through the water column (see 5.2.3 below).

5.2.1 Field Methods

The protistan communities in the water column and sediment traps were sampled at approximately weekly intervals between December 1997 and March 1998 in Middle Basin, Ellis Fjord. The method of sampling the water column has been outlined in Chapter 3, and the sediment trap design and sampling protocol provided in Chapters 2 & 4. The fjord remained ice-covered during this study. However, ice thickness ranged between 2.5 & 1 m, indicating substantial surface and under-ice melt. For further description of the physical characteristics of the site see Chapter 1.

5.2.2 Laboratory methods

5.2.2.1 Sample preparation

Each 2 L water sample was mixed, and a 500 ml aliquot from each replicate Kemmerer bottle sample was decanted into a measuring cylinder and fixed with acid Lugol's iodine. Samples were sedimented for ≥24 hours and the

supernatant removed by aspiration. The remaining sample (approximately 20 ml) was transferred to a glass, capped container and refrigerated at 0-4°C prior to microscopic analysis.

The samples in the collector tubes of the sediment traps, which had been fixed in a mercuric chloride / brine solution, were gently mixed, and a 40 ml subsample (approximately 1/5 of the total sample) decanted from each replicate sample into a measuring cylinder and preserved in acid Lugol's iodine. Samples were left for approximately 24 hours and prepared as above.

The use of different fixatives for the initial fixation of suspended protist samples and those collected in sediment traps could result in disparities between the suspended and sedimented protistan assemblages. While Lugol's iodine, like other fixatives (e.g. formalin, formaldehyde, and glutaradlehyde) can result in the loss of protist cells, it is reportedly preferable to other fixatives for the fixation of cilliates (Ohman & Snyder 1991, Sherr & Sherr 1993, Leakey et al. 1994). Few studies have examined the effects of mercuric chloride on protistan species. However, my observations suggest that mercuric chloride in a brine solution does not cause significant lysis of most protistan cells (see Chapter 2). Further, Pace & Orcutt (1981) reported that the fixation of protists using mercuric chloride was comparable to that using Lugol's iodine.

5.2.2.2 Microscopy and data analysis

Protists were settled in Utermöhl sedimenting chambers, identified and counted at 400 x magnification using phase contrast optics on a Leitz Fluovert inverted microscope. As for Chapter 4, only samples obtained during January and February were analysed as chlorophyll *a* concentration in the water column indicated peak biomass during these months (see Chapter 3, Figure 3.2). Two of the three independent replicate samples were analysed for each sampling date due to the time involved in such detailed anaylses. Fifteen replicate fields (or portions thereof) were counted per sample, as this was shown to reduce the variance between fields and provide a reliable estimate of the mean, and the mean and standard error calculated. Dominant protist taxa were identified to species where possible and to genus

or class where light microscopy did not allow detailed identification (see Chapter 3).

Protist taxa were categorised according to cell size to investigate their size-fractionated contribution to vertical flux. The mean size of each protistan taxon was calculated by measuring up to 100 cells for an individual species using a stage micrometer under an inverted microscope. Cells were classified as micro- or nanoplanktonic if most cell lengths were >20 μm or <20 μm, respectively. Autotrophic flagellates were determined by their taxonomic identity, the presence of chloroplasts, and iodine staining of starch granules. Dinoflagellates were grouped as autotrophic or heterotrophic according to Tomas (1996), and mixotrophic species were included in both groups.

The percentage daily loss rate (L) of protists at depth intervals throughout the water column was calculated following the method of Taguchi and Hargrave (1978) as simplified by Anadón et al. (2002).

$$L = (Sd/Sp) \times 100 \qquad \text{(Equation 5.1)}$$

where Sd was the sedimentation rate m^{-2} day^{-1} and Sp the suspended stock m^{-2}.

5.2.3 Statistical analysis

Protist concentrations were integrated from surface to depths of 5, 10, 20 & 40 m in the water column, and between depths (e.g. 5-10, 5-20, 5-40 m). The data were log (x+1) transformed to normalise the distributions of the data and to ensure homogeneity of variances. Linear regressions were performed between the integrated protistan concentration in the overlying water column and the concentration of protists in traps at each depth (e.g. the integrated concentration of protists from 20-40, 10-40, 5-40, & 0-40 m was regressed upon the protistan concentration in traps at 40 m). The correlation coefficient (r) was used to determine the statistical significance of these relationships at $\alpha = 0.05$.

5.3 Results

5.3.1 Water column

5.3.1.1 Microplankton

The diatoms *Fragilariopsis curta, Fragilariopsis cylindrus,* and *Nitzschia lecontei* comprised most of the microplankton in the water column. Their concentration in the upper 10 m was high during January but declined thereafter (Figure 5.1a). Diatom species composition remained largely unchanged throughout the season. However, at the end of February *Pinnularia quadratarea* v. *constricta* and *Entomoneis kjellmanii* appeared at concentrations around 3.49 x 10^6 cells m^{-3} in near-surface waters (≤10 m depth) (see Chapter 3). These species were also observed in ice-core samples collected at the site in early December (see Chapter 3).

Autotrophic dinoflagellates were dominated by *Gymnodinium* spp., including *Polarella glacialis,* as well as the mixotrophic *Ceratium* spp. They were observed in low concentration throughout January but increased in concentration during February at all depths, reaching 1.81 x 10^8 cells m^{-3} at ≤10 m (Figure 5.1b). Heterotrophic dinoflagellates (HDIN) largely comprised the genera *Gyrodinium, Amphidinium,* and *Ceratium.* HDIN also occurred in low concentration throughout January, but showed a peak in early February at ≤5 m (6.33 x 10^7 cells m^{-3}) (Figure 5.1b). Thereafter, concentrations of HDIN decreased in near-surface waters (≤10 m depth) but increased at ≥20 m. Ciliates, comprising *Strombidium* spp., oligotrich genera, and tintinnids, were present throughout the water column during February, reaching concentrations of 3.96 x 10^7 cells m^{-3} at ≤5 m in mid February (Figure 5.1b).

5.3.1.2 Nanoplankton

Autotrophic flagellates dominated the nanoplankton in the water column. An unidentified cryptophyte comprised most of the flagellate concentration. This cryptophyte first appeared at 40 m on 11 January and penetrated to shallower depths in the water column to peak at 6.44 x 10^9 cells m^{-3} at ≤5 m on 25 January (Figure 5.1c). Following its decline at ≤5 m, the cryptophyte concentration increased at ≥20 m on 1 February.

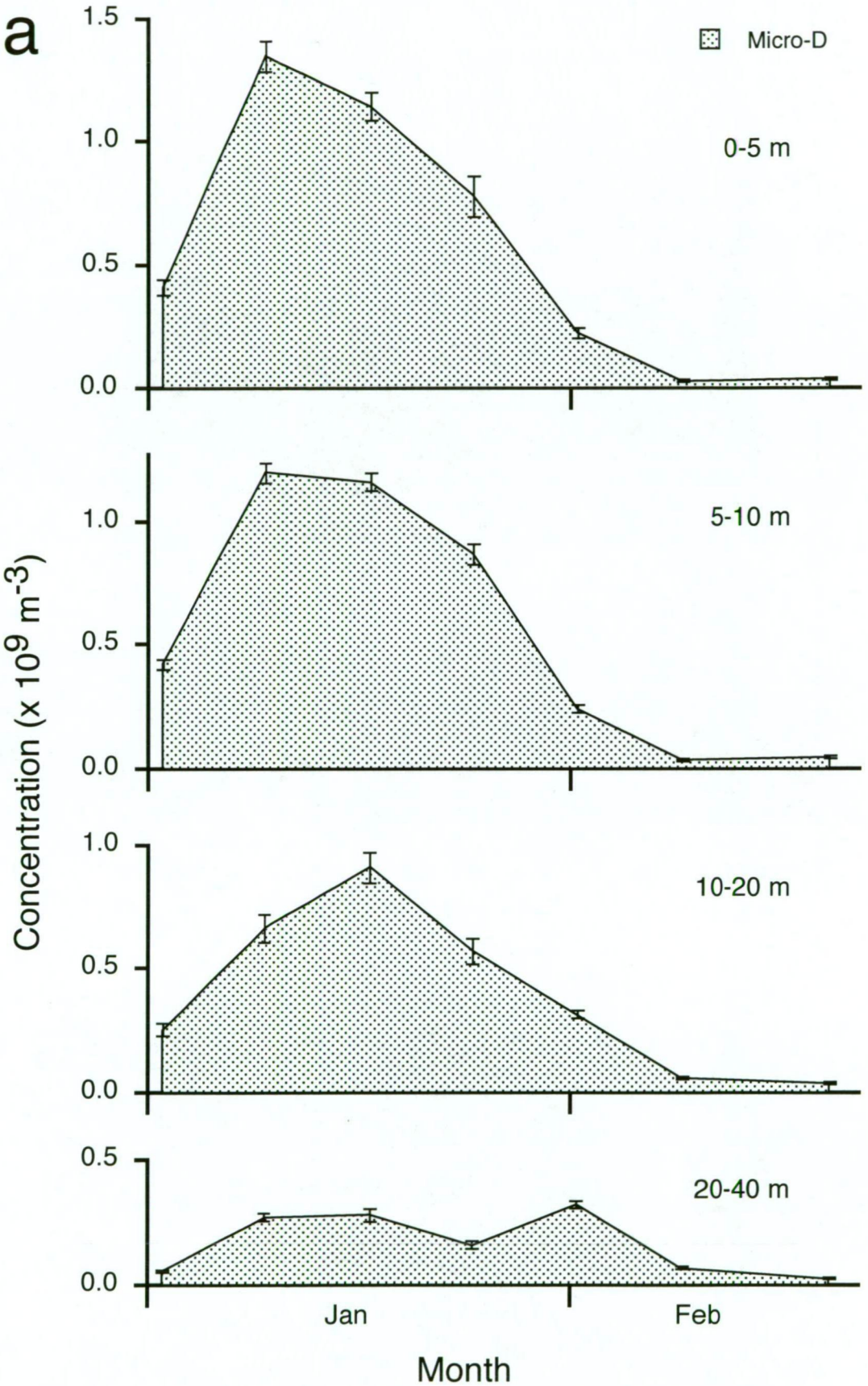


Figure 5.1a. The integrated concentration of microplanktonic diatoms (Micro-D) from 0-5 m, 5-10 m, 10-20 m, and 20-40 m in the water column. Error bars represent ± 1 SE.

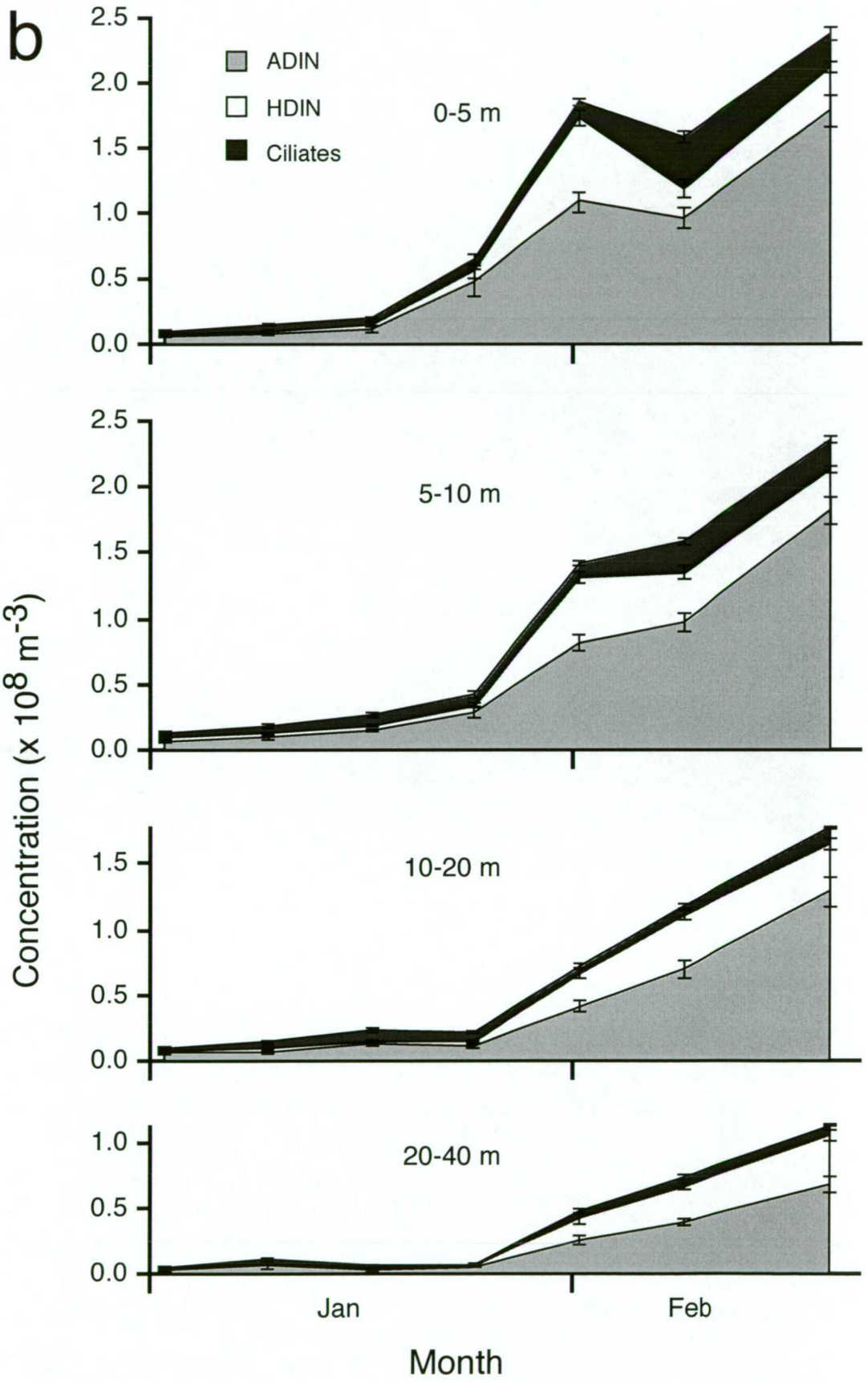


Figure 5.1b. The integrated concentration of other microplankton (ADIN and HDIN represent auto- and heterotrophic dinoflagellates) from 0-5 m, 5-10 m, 10-20 m, and 20-40 m in the water column. Error bars represent ± 1 SE.

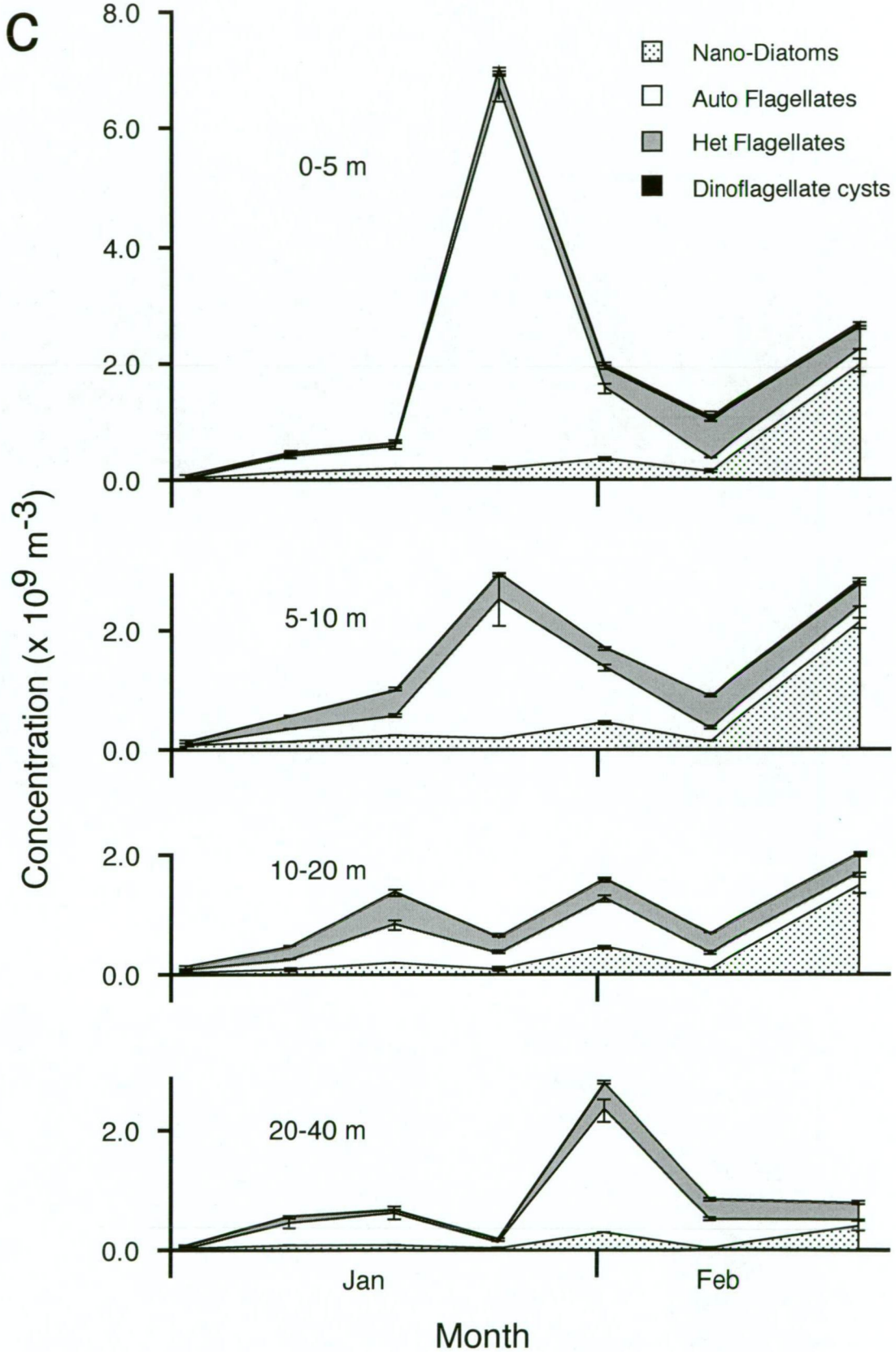


Figure 5.1c. The integrated concentration of nanoplankton from 0-5 m, 5-10 m, 10-20 m, and 20-40 m in the water column. Error bars represent ± 1 SE.

Nanoplanktonic diatoms peaked in concentration at the end of February in the upper 10 m of the water column. The majority of this peak was due to *Fragilariopsis pseudonana* but small *Thalassiosira* spp. also contributed substantially to this high concentration.

Heterotrophic flagellates were abundant throughout the water column, reaching highest concentrations during February. Dinoflagellate cysts were generally in low concentration throughout the water column, but, like heterotrophic flagellates, increased in concentration throughout February (Figure 5.1c).

5.3.2 Sediment traps

5.3.2.1 Microplankton

Diatoms, especially *Fragilariopsis curta* and *Fragilariopsis cylindrus*, dominated the protist assemblage in sediment traps at all depths throughout most of the season. Highest fluxes were observed at ≤10 m, except towards the end of February when diatom flux declined in upper waters (Figure 5.2a). This decline coincided with an increase in their concentration at ≥20 m. In early January, the diatom species *Entomoneis kjellmanii, Pinnularia quadratarea* v. *constricta,* and *Pleurosigma* spp. were observed in sediment traps at all depths, however their flux was low (around 8.36×10^5 cells m^{-2} day^{-1}). *Pinnularia quadratarea* v. *constricta* also occurred in traps at ≥20 m during late February (Table 5.1). These species had previously been observed in ice core samples collected in December (see Chapter 3).

The flux of autotrophic dinoflagellates showed a substantial peak in the traps at ≤10 m during early February (2.19×10^6 cells m^{-2} day^{-1} at 10 m) and subsequently increased in traps at lower depths over the month (Figure 5.2b). The flux of heterotrophic dinoflagellates was much lower (5.64×10^5 cells m^{-2} day^{-1} at 10 m) than that of the autotrophic species, but showed a similar temporal pattern. The abundance of ciliates in sediment traps was negligible.

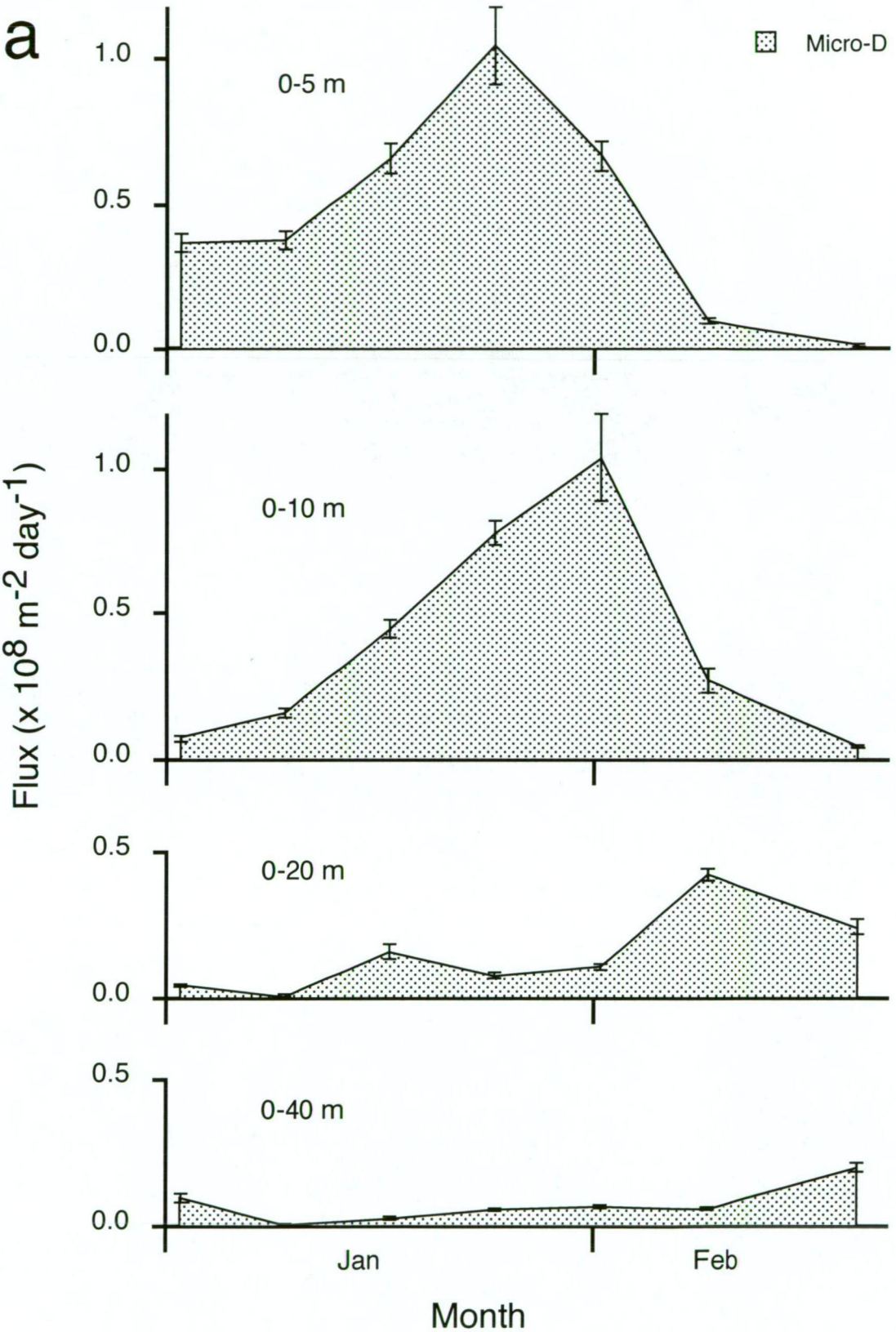


Figure 5.2a. The flux of microplanktonic diatoms (Micro-D) from 0-5 m, 5-10 m, 10-20 m, and 20-40 m in the water column. Error bars represent ± 1 SE.

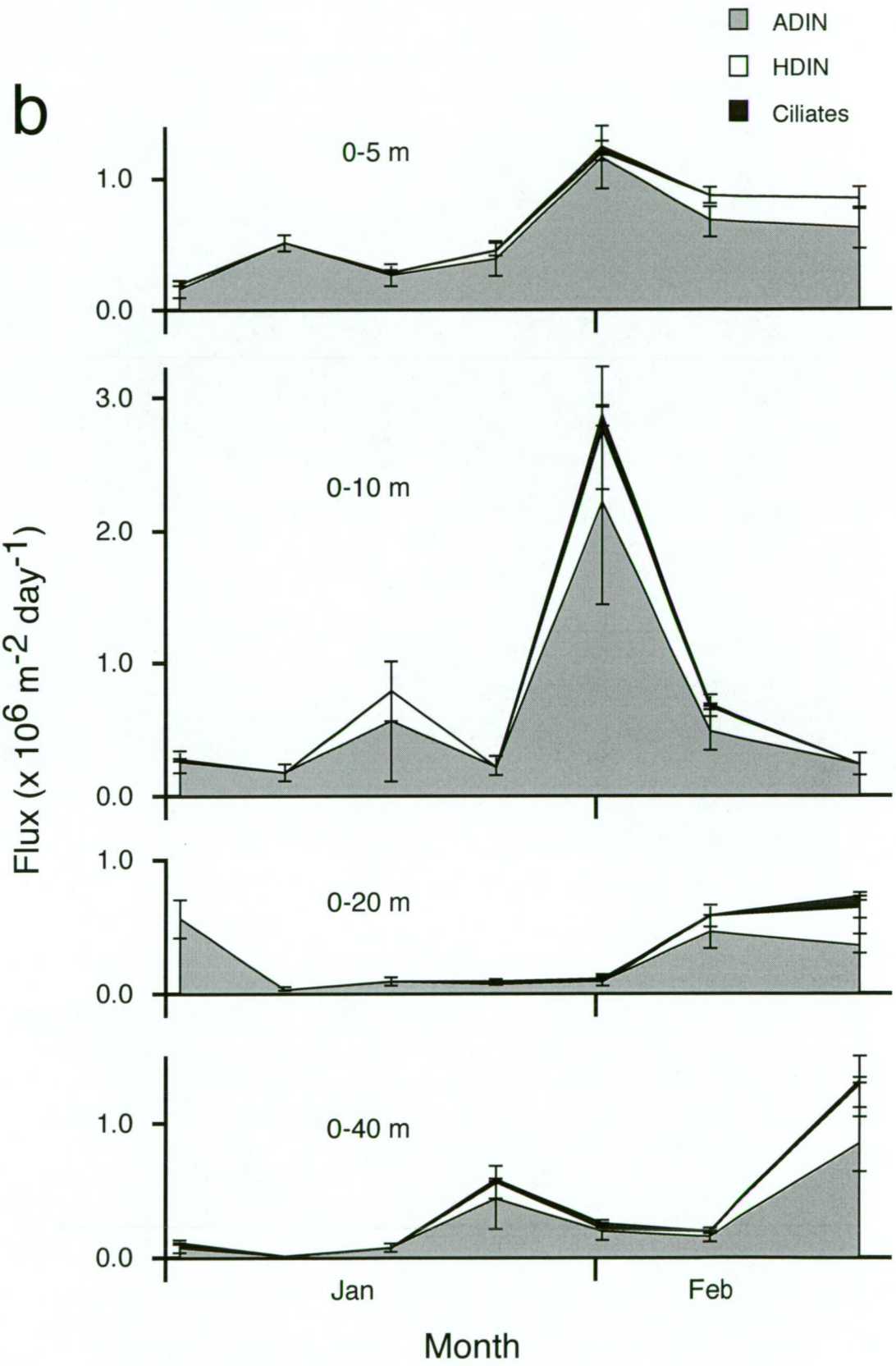


Figure 5.2b. The flux of other microplankton (ADIN and HDIN represent auto- and heterotrophic dinoflagellates) from 0-5 m, 5-10 m, 10-20 m, and 20-40 m in the water column. Error bars represent ± 1 SE.

Table 5.1. Mean (± SE) flux of ice-associated diatoms (x 10^4 m^{-2} day^{-1}) at depth intervals from surface to 40 m. *Entomoneis kjellmanii* and *Pleurosigma* spp. were not present in traps beyond early January.

Species	Date	0-5 m	0-10 m	0-20 m	0-40 m
Pinnularia quadratarea v. *constricta*	4 Jan	2.65 ± 2.65	1.33 ± 1.33	10.6 ± 5.03	25.2 ± 7.12
	11 Jan	0.00 ± 0.00	29.2± 9.08	0.44 ± 0.44	0.00 ± 0.00
	18 Jan	2.50 ± 2.50	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
	25 Jan	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	13.3 ± 5.17
	1 Feb	5.16 ± 3.59	0.00 ± 0.00	0.00 ± 0.00	1.99 ± 1.46
	8 Feb	6.63 ± 3.86	5.01 ± 5.01	0.00 ± 0.00	3.10 ± 1.87
	18 Feb	5.57 ± 3.10	8.87 ± 5.13	3.61 ± 2.51	1.75 ± 1.75
Entomoneis kjellmanii	4 Jan	10.6 ± 5.03	19.9 ± 8.26	23.9 ± 10.9	11.9 ± 3.56
	11 Jan	2.50 ± 2.50	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Pleurosigma spp.	4 Jan	0.00 ± 0.00	5.31 ± 3.69	2.65 ± 2.65	7.96 ± 2.74

5.3.2.2 Nanoplankton

Heterotrophic flagellates dominated the flux of nanoplankton at all depths throughout the season. However, peak fluxes (between 1.25 and 2.06 x 10^7 cells m^{-2} day^{-1}) were observed at ≤ 10 m in early January and throughout February. In contrast, autotrophic flagellates were only present in 5 m traps at the end of January, reached a peak flux of 4.54 x 10^6 cells m^{-2} day^1 in early February, and declined thereafter (Figure 5.2c). Nanoplanktonic diatoms, mainly *Thalassiosira* spp. were also observed in traps, mostly at ≤5 m from the end of January onwards. The flux of these diatoms increased during late February largely due to an increase in the flux of *Fragilariopsis pseudonana* (Figure 5.2c). The fluxes of dinoflagellate cysts were generally low, though a small peak was observed at ≤5 m in early January.

5.3.3 Protistan contribution to vertical flux

Microplanktonic diatoms contributed most of the vertical flux, especially later in the season when 3.5% and 1.3% of the suspended stock was lost per day, from 0-20 m and 0-40 m respectively (Figure 5.3a). Overall, their contribution to vertical flux was greatest at ≤10 m throughout the season and resembled the observed pattern of flux recorded in sediment traps (Figure 5.2a). The contribution by other microplankton to vertical flux was <1 % and

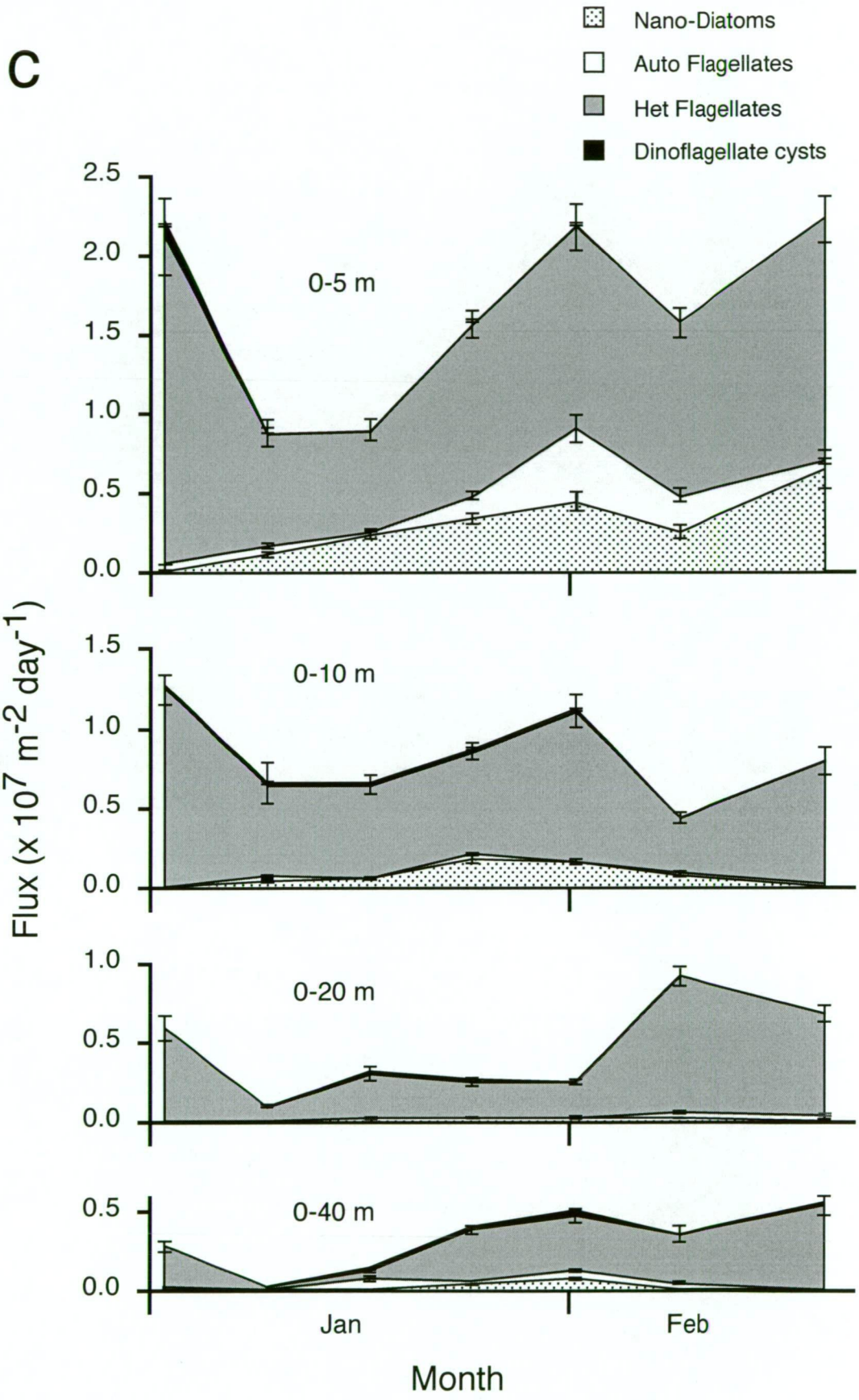


Figure 5.2c. The flux of nanoplankton from 0-5 m, 5-10 m, 10-20 m, and 20-40 m in the water column. Error bars represent ± 1 SE.

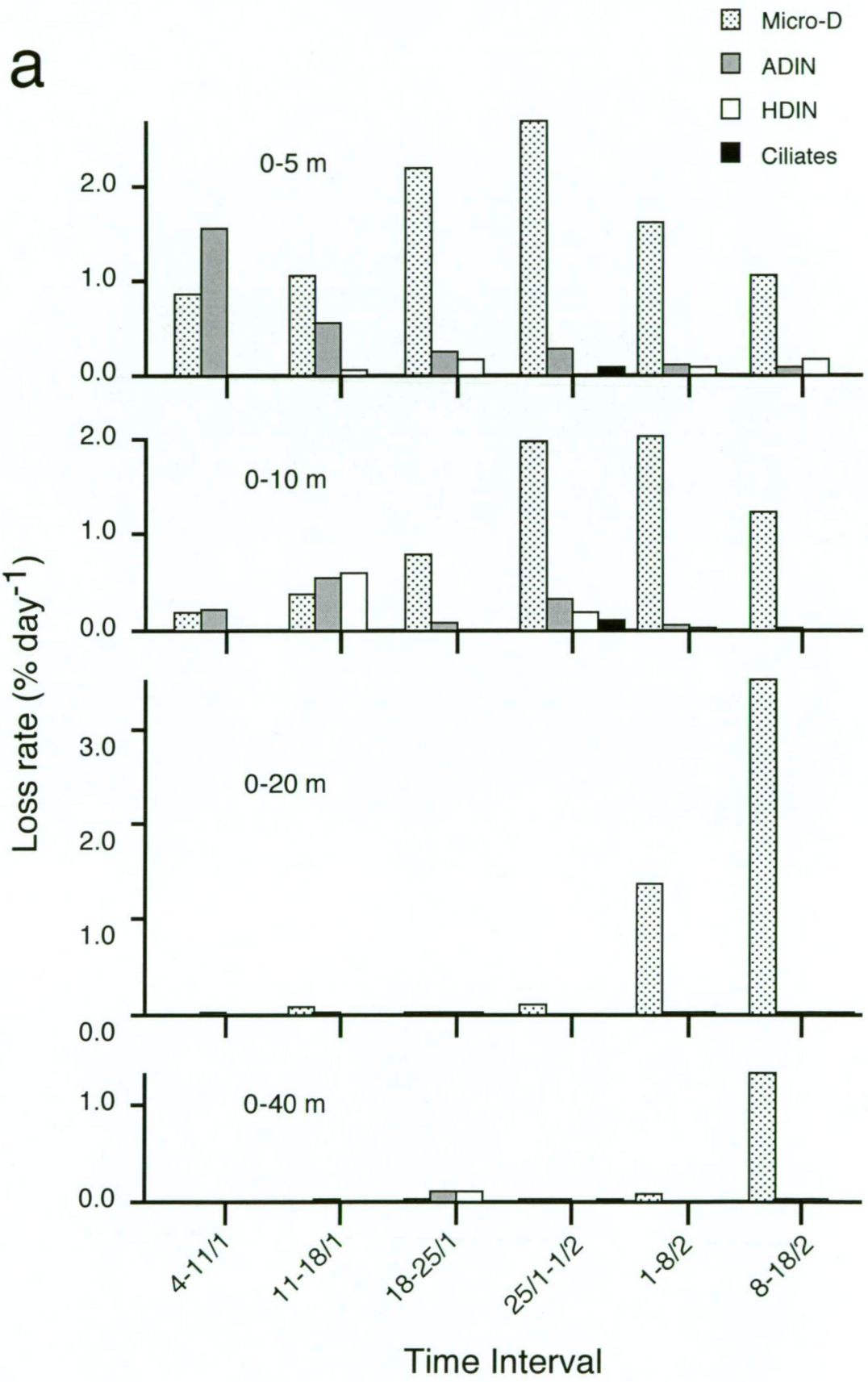


Figure 5.3a. The percent loss of microplankton (Micro-D = Microplanktonic diatoms, ADIN & HDIN = auto- and heterotrophic dinoflagellates) with depth through the water column.

remained relatively constant, with the exception of ADIN that contributed 1.6% during early January at 0-5 m.

Heterotrophic flagellates were the second greatest contributor to vertical flux, with >2 % of the population lost per day from 0-5 m during early to mid January (Figure 5.3b). However, their contribution declined during February to <1% loss of the suspended stock per day from 0-5 m. Other nanoplankton contributed little to vertical flux throughout the season, with losses of <0.5% of the population per day. Overall, excepting microplanktonic diatoms, the protistan community made a negligible contribution to vertical flux below 10 m.

5.3.4 Statistical analysis

Attempts to relate the concentration of protists in the water column with their abundance in sediment traps showed few significant correlations (Table 5.2), although the concentration of micro and nano-planktonic diatoms and ADIN at ≤5 m in the water column did correlate with their respective flux to 5 m depth. HDIN concentration at depth intervals from 0-20 m in the water column significantly correlated with HDIN flux to 20 m, and the concentration of dinoflagellate cysts from 5-10 m showed a negative relationship with the flux of cysts to 10 m depth. However, as both HDIN and dinoflagellate cysts were largely absent from sediment traps at 10 & 20 m these correlations are likely to be spurious.

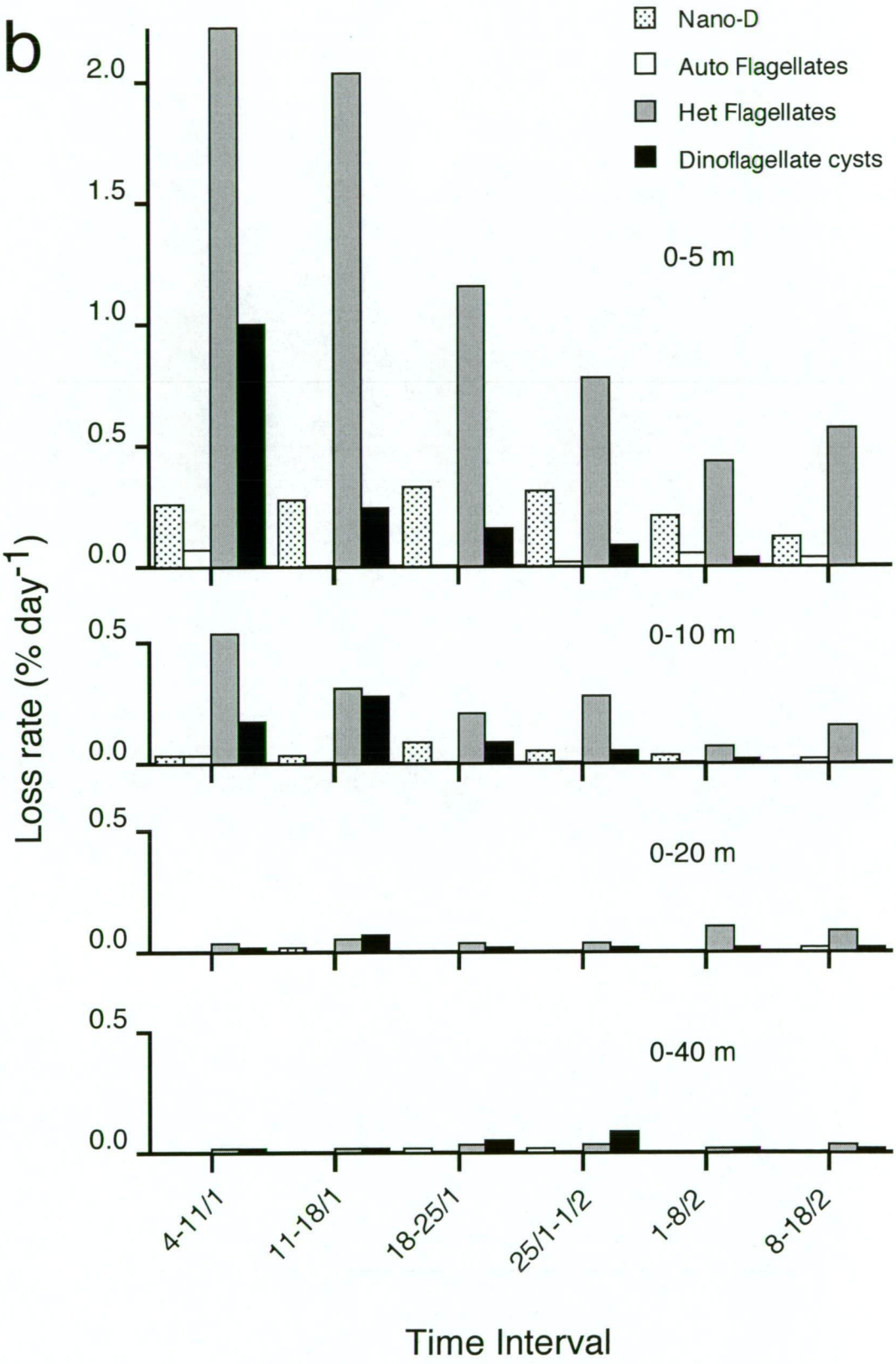


Figure 5.3b. The percent loss of nanoplankton (Nano-D = Nanoplanktonic diatoms) with depth through the water column.

Table 5.2. Significant correlations between protistan concentrations in the water column (m^{-2}) and in sediment traps (m^{-2} day^{-1}). Micro-D & Nano-D = micro- and nanoplanktonic diatoms, respectively. ADIN & HDIN = auto- and heterotrophic dinoflagellates, respectively. D-cysts = Dinoflagellate cysts.

Protist taxon	Water column above trap depth	Trap Depth	r	n	Probability	Slope
Micro-D	0-5	5	0.813	7	0.02<p<0.05	+
ADIN	0-5	5	0.773	7	0.02<p<0.05	+
HDIN	0-20	20	0.862	7	0.01<p<0.02	+
	5-20	20	0.831	7	0.02<p<0.05	+
	10-20	20	0.813	7	0.02<p<0.05	+
Nano-D	0-5	5	0.837	7	0.01<p<0.02	+
D-cysts	5-10	10	0.853	7	0.01<p<0.02	-

5.4 Discussion

Despite very high primary production in Antarctic coastal waters, little is known about the immediate fate of this production, nor the role of heterotrophic protists in vertical flux (Karl et al. 1991). It has been generally accepted that microplanktonic, heavily silicified cells sink, while nanoplanktonic cells remain suspended in the water column (Smayda 1970, Ittekot 1996, Smetacek 2000). However, recognition of the role of aggregates in vertical flux, which are hotspots of microbial activity, is challenging this view (Michaels & Silver 1988, Michel et al. 1997, Azam 1998, Andreassen et al. 1999). In addition, cell physiology and species life-history strategies play a role in determining whether cells remain in suspension in upper waters or sink (Smetacek 1985, Waite et al. 1992, Kiørboe 1993). However, the role of plankton ecology in determining the magnitude of vertical carbon flux is rarely considered by biogeochemists in studies examining temporal changes in this flux (e.g. Billet et al. 1983, Wefer & Fischer 1988, Cailliau et al. 1999). Here, I discuss the contribution by micro- and nanoplanktonic protistan assemblages to vertical flux. I determine the species composition and magnitude of the suspended assemblage that sediments, and the factors that regulate this flux throughout an Antarctic summer.

5.4.1 Ice-algae

The concentration of ice-associated microplanktonic diatoms in the water column was negligible during early January. However, brief, though significant, fluxes of these diatoms were observed below 5 m, and dominated the composition at lower depths (20 & 40 m). These ice-algae were large and heavily silicified. However, their flux to depth was largely determined by the timing of ice-melt, as they did not contribute to the planktonic diatom bloom. In addition, ADIN and their nanoplanktonic cysts were observed in the ice-algal assemblage (see Chapter 3) and, like the ice-associated diatoms, their concentrations in the water column were negligible but their flux was high in near-surface waters during early summer. This indicates that both micro- and nanoplanktonic protists rapidly sank through the water column and/or were subjected to high grazing pressure by metazoa (see Chapter 3). Further, this could be an artefact of the sampling methods as the release of ice-algae into the water column is usually sporadic. Thus, the chance of sampling ice-algae would be greater in sediment traps that were deployed over a week, than in water bottle samples that were obtained on a single day.

5.4.2 Planktonic algae

In contrast to ice-associated protists, much of the planktonic diatom biomass in early January did not sediment beyond 10 m. Diatom concentrations increased rapidly between early and mid-January, and fast-growing phytoplankton are reportedly more buoyant (Smetacek 1985, Waite et al. 1992, Kiørboe 1993). As diatoms senesce they lose buoyancy and become 'sticky', which can lead to the formation of fast-sinking aggregates (marine snow) (Riebesell 1991, Waite et al. 1992, Kiørboe & Hansen 1993, Becquevort & Smith 2001). Algal clumps were observed in water samples at various times throughout the season. However, it was not possible to determine the abundance of aggregates in traps due to the inability to differentiate between what sank as aggregates and aggregation that occurred within traps. Nonetheless, peak diatom sedimentation at ≤10 m occurred during the decline and, presumably, senescence of the diatom bloom during late January / early February.

Nanoplanktonic protists were dominated by flagellates that reportedly have low sinking rates due to their small size (Smayda 1970), and tend to dominate in stratified waters where they remain suspended, lyse, or are remineralised by microzooplankton or bacteria (Kiørboe 1993, Gibson 1998). Consequently, they are often absent from trap material and are not considered to contribute to vertical flux (Kiørboe 1993). However, I found that heterotrophic nanoflagellates contributed substantially to flux (second only to diatoms). Attraction of heterotrophs and their growth within traps has been reported (Taylor et al. 1986, Lee et al. 1992). However, my traps were poisoned with mercuric chloride, which caused complete mortality of flagellates in the laboratory (see Chapter 2).

Similar to the ice-algae, high concentrations of heterotrophic nanoflagellates were observed in traps during early January, despite their low concentration in the water column. Ice-algal aggregates are colonised by microbes and support high growth rates of heterotrophic nanoflagellates (Caron 1991, Patterson et al. 1993). Therefore, ice-algal aggregates may have assisted the flux of heterotrophic nanoflagellates to depth. The highest flux of heterotrophic nanoflagellates occurred during February when diatom senescence is likely to have caused aggregation (see above) and protozoa dominated the protist community. While the general belief is that communities of heterotrophic nanoplankton contribute to respiration in near-surface waters, my study indicates that their role was not confined to the microbial loop, in that they also contributed to vertical flux.

Despite the seasonal succession of protists from a dominance of autotrophs (mostly diatoms) to a more heterotrophic and microbially-based community (see Chapter 3), microplanktonic diatoms dominated flux throughout the sampling period. Few studies have used microscopy to examine, in detail, the seasonal succession of the protistan community while simultaneously determining the contribution by individual taxa and species to flux. However, those studies that have undertaken such analyses have reported that diatoms dominated protistan flux regardless of the suspended community composition (Sasaki & Hoshiai 1986, Gibson 1998, Horn & Horn 2000). The minor contribution to flux by microplanktonic protozoa is expected due to their motility and low concentration, although poisoned traps have previously been reported to overestimate protozoan

concentrations due to the trapping of these organisms during their migration through the water column (Olesen 2001). This was not apparent in my study, and only heterotrophic nanoflagellates contributed substantially to vertical flux (see above).

5.4.3 The contribution by the suspended protistan assemblage to vertical flux

While microplanktonic diatoms dominated flux, their rapid decline in the water column was not entirely reflected in their concentration in traps, with a maximum rate of only 3.5% of the diatoms lost per day from 0-20 m. The equation for the loss rate of suspended protists from the water column assumes a direct temporal relationship between the concentration of suspended and sedimented protists. However, I recorded a lag of approximately two weeks between the water column bloom and sedimentation, and this has similarly been reported in other coastal and enclosed water bodies (Horn & Horn 2000, Olesen 2001). Therefore, the loss rate of suspended protists may not provide an accurate indication of protistan flux. Nonetheless, overall concentrations of sedimented protists were substantially lower than those suspended in the water column and the cell loss rates I calculated are within the range of values reported for the Antarctic peninsula (Anadón et al. 2002). They are also comparable to the loss of chlorophyll *a* reported in other coastal waters (Taguchi & Hargrave 1978, Olesen 2001).

Losses of suspended nanoplankton to depth generally only occurred to 5 m and were very low, except for dinoflagellate cysts and heterotrophic flagellates that, at times, contributed substantially to vertical flux. This is reflected by the relatively high loss rate (>2%) of the flagellate stock during early summer. While highest fluxes of heterotrophic flagellates occurred during February, these fluxes were not reflected in the calculated percentage loss rates due to their concurrent high concentrations in the water column.

Such low loss rates of suspended plankton to depth are in keeping with the finding that only a small percent of the total production in the ocean is lost by sinking (Wassmann 1998). The fate of primary production that does not

sink to depth is poorly understood but is possibly determined by physical and trophic dynamics (Goldman 1988, Legendre & Le Fèvre 1989, Wassmann et al. 1991, Tréguer 1994). High concentrations of copepods and faecal pellets were observed during January (see Chapter 4), and it is likely that, in addition to cell lysis and decay, their grazing reduced the diatom flux. However, I did not measure any physical parameters or processes, such as lateral advection, that could also have contributed to the observed decline in the suspended stocks during mid to late summer.

While much of the diatom biomass was retained in the upper 10 m of the water column, only the relationships between the concentration of diatoms at ≤5 m and diatom flux to 5 m depth were statistically significant. This may have resulted from a switch in grazing pressure by microheterotrophs from the suspended phytoplankton community to the under-ice-algae. Therefore, the majority of the suspended phytoplankton stock at ≤5 m was available to sediment. No other significant correlations were observed between the suspended concentrations of protists and their flux to depth. Similarly, a lack of correlation between phytoplankton standing stocks and vertical flux has been observed in the Bransfield Strait, Antarctica (von Bodungen et al. 1987, Karl et al. 1991). This general lack of correlation appears to result from the temporal uncoupling of production and flux (see 5.4.2 Planktonic algae), which has been commonly reported in Antarctic waters (Dunbar et al. 1989, Asper & Smith 1999, Becquevort & Smith 2001). Therefore, short-term cruises that take 'snapshots' of the water column often have difficulties in directly linking production and flux (Michaels & Silver 1988, Asper & Smith 1999).

5.5 Concluding remarks

It is generally believed that communities dominated by microplanktonic diatoms will result in carbon export to depth, while those dominated by nanoplankton and microheterotrophs will result in respiration and retention in upper waters (Michaels & Silver 1988, Bathmann 1996, Froneman & Perissinotto 1996). However, this study has shown that micro- and nanoplanktonic protists can both contribute to remineralisation and vertical flux, as the size of individual taxa does not directly determine their fate. Rather, it is the cell physiology combined with physical processes, primarily ice-melt and aggregation in this study, as well as grazing, which determines

protistan flux. This often results in poor temporal coupling between the composition of the suspended assemblage and that which contributes to vertical flux (Dunbar et al. 1989, Asper & Smith 1999, Becquevort & Smith 2001). Such taxonomic-specific characteristics have not been considered in most studies investigating temporal changes in the magnitude of carbon flux (e.g. Billet et al. 1983, Wefer & Fischer 1988, Cailliau et al. 1999). However, recognition of the ecological traits of protists and their interactions with the physical and biotic environment is vital if we are to understand how changes in the protistan community composition, resulting from global warming, will affect the magnitude of atmospheric carbon that can be sequestered by the world's oceans.

Chapter 6

The role of phytoplankton and microzooplankton in biogenic carbon flux

6.1 Introduction

To predict future changes in global carbon flux it is necessary to understand the mechanisms that determine the export or retention of production in the oceans (Legendre & Le Fèvre 1989, Peinert et al. 1989, Le Fèvre et al. 1998). These are determined by the physical structure of the water column, and the composition and trophodynamics of the plankton community (Legendre & Rassoulzadegan 1996, Froneman et al. 1997, Saggiomo et al. 1998, Tian et al. 2001). Melting sea-ice promotes changes in the physicochemical structure of the water column during spring/summer that lead to large blooms of phytoplankton in Antarctic waters. These blooms can be regenerated by microbial processes in the water column, or exported to depth via the direct sedimentation of phytoplankton cells or the sedimentation of zooplankton faecal pellets (Smetacek et al. 1990, Froneman & Perissinotto 1996, Serret et al. 2001, Turner 2002). Despite the pivotal role of grazing in determining whether production is exported or regenerated, the role of zooplankton in vertical flux is surprisingly poorly understood (Banse 1994, Wassmann 1998). To define this role requires an understanding of species-specific ecologies and interactions that determine the structure and trophodynamics of plankton communities, and thereby the regulation of vertical carbon flux (Aksnes & Wassmann 1993, Kang & Lee 1995).

Models can assist in elucidating how ecosystem processes determine the magnitude of carbon flux. However, they are only as realistic as the data upon which they are based (Paffenhöfer 1998, Brush et al. 2002). Most models use broad compartments in order to reduce the complexity down to manageable proportions, but in doing so lose considerable biological detail and accuracy (Brush et al. 2002). For example, models use data from numerous studies where the methods may not be comparable, and establish

broad taxonomic groups that can mistakenly group organisms that have dissimilar trophic roles (e.g. Huntley et al. 1991, Banse 1995b, Walsh et al. 2001). Such generalisations can substantially affect the magnitude of carbon flux and obscure the regulatory role of individual taxa. Thus, the relative importance of the direct sedimentation of phytoplankton versus grazer-mediated flux remains poorly understood.

In this chapter, I develop models of carbon flux through the top 40 m of the Ellis Fjord ecosystem, based on site and species-specific data, to examine how changes in the physical environment and trophic structure over summer affects the direct sedimentation of phytoplankton versus the role of microzooplankton grazing in vertical carbon flux.

6.2 Methods

The data presented here for protists, copepods, and faecal pellets are based on the concentrations and fluxes presented in Chapters 3, 4 & 5. For the purposes of this chapter, only data obtained for January and February are used, to enable comparisons with protist data and calculation of carbon fluxes.

The data are presented for the upper 10 m and the lower 10-40 m of the water column. This depth separation was determined according to statistical analyses that showed differences in the plankton community composition (see Chapter 3), and observations of changes in protist and faecal pellet flux (see Chapters 4 & 5). Data for the lower 10-40 m of the water column were calculated by subtracting integrated data for 0-10 m from that of 0-40 m. No standard errors are presented as they could not be calculated on integrated nor subtracted data. Any negative values that resulted from the subtraction were changed to zero.

6.2.1 Primary production and plankton biomass

Primary production was calculated using a production:biomass conversion of 1.359 mg C d^{-1} mg C^{-1} based on primary production and phytoplankton biomass (chlorophyll *a*) measured under ice-cover at a nearby coastal site (Swadling et al. 1997). Protistan biomass was determined by measuring up

to 100 cells of each species, depending on their abundance, and calculating the mean dimensions. These measurements were used to calculate the mean cell biovolume according to the cell geometrical shape (Appendix 4). Cell biovolume was converted to cell carbon using the equations established by Menden-Deuer & Lessard (2000); for diatoms,

$$pgC\ cell^{-1} = 0.288 \times volume^{0.811} \qquad \text{(Equation 6.1)}$$

and for other protists,

$$pgC\ cell^{-1} = 0.216 \times volume^{0.939} \qquad \text{(Equation 6.2)}$$

Protists were grouped as micro and nanoplankton according to cell size, and as phytoplankton or protozoa as described in Chapter 4.

Following my approach in Chapter 4, the copepod biomass was determined only from the concentrations of the four dominant species. Copepod biomass, except for harpacticoids, was determined using species-specific carbon concentrations in Swadling et al. (1997) that had been corrected for 30% weight loss due to preservation in formaldehyde and were based upon a carbon conversion of 50 % of corrected dry weight (Båmstedt 1986, Böttger & Schnack 1986). The unidentified harpacticoids in this study were much smaller than those recorded by Swadling et al. (1997), so I used the average dry weights of small harpacticoids reported from Ellis Fjord (Kirkwood 1993). These weights were corrected for loss due to preservation and converted to carbon as above.

6.2.2 Faecal pellet carbon content

Faecal pellets from a sediment trap sample were pipetted into a measuring cylinder and oval copepod pellets and protozoan pellets were separated by differential sedimentation. Pellets were subsequently picked with a micro-pipette attached to a modified syringe while viewed under a dissecting microscope. The pellets were rinsed in a petri dish containing filtered sea-water until they were free from extraneous organic matter. Approximately 300 pellets of each type were pipetted onto precombusted 13 mm GF/F filters, rinsed with Milli-Q water under a vacuum of 250 mM Hg, and left for approximately 3 minutes to remove excess water and salts. Samples were fumed in an acid bath for ≥24 h, then oven dried at 60°C for ≥24 h. Filters containing pellets were folded in half and placed in a precombusted aluminum foil sachet and sealed in plastic bags for later analysis. Samples

were analysed using an Exeter Analytical CHN instrument at Horn Point Laboratory, University of Maryland Systems, Maryland, USA.

Problems in identifying and isolating cylindrical pellets and minipellets precluded direct CHN analyses (see Chapter 4). For cylindrical pellets, a conversion of 0.04 pg C μm^{-3} was used, based on measurements of cylindrical pellets produced by mesozooplankton under 100% ice-cover in the Barents Sea (Urban-Rich 1997). To my knowledge the only carbon conversion established for minipellets in the literature is a value of 0.01 mg C mm^{-3} by Buck et al. (1990). While some of the minipellets observed in this study were morphologically similar to those in Buck et al. (1990), others were not (see Chapter 4). Therefore, I determined carbon to volume conversion factors using the measured carbon values obtained in this study for oval copepod and large protozoan pellets and these conversion factors were used to determine the carbon content of minipellets of similar morphology.

6.2.3 Particulate organic carbon

The method for the determination of POC concentration is described in Chapter 2.

6.2.4 Models of carbon flux

The season was separated into two time periods, identified by cluster and ordination analyses, that showed a substantial shift in the dominant food web during the season (see Chapter 3). The 'early' part of the summer represented the first three weeks in January, while the 'late' summer comprised the last week in January and first three weeks in February. Data were averaged over each time period to provide an estimate of biomass and flux. The depth separation in the models has already been described (see above).

To my knowledge, no GGEs have been empirically determined for Antarctic protozoa. Therefore, protozoan gross growth efficiencies (GGEs) were determined from the median of literature values reported for temperate taxa grazing similar food types and concentrations to that available in Ellis Fjord (Table 6.1). To obtain an overall GGE for protozoa, the proportion of biomass of each taxon was multiplied by the growth efficiency, and the efficiencies of the species were summed.

Table 6.1. Taxa-specific gross growth efficiencies (GGE) of protozoa based on similar genera, and food quality and quantity to that in Ellis Fjord. Nf = Nanoflagellates, Cy = Cynaobacteria, Coc = Coccolithophorids, Crypto = Cryptophytes Pr = Prymnesiophytes, Bact = Bacteria, concn n.s. = Concentration not specified, 1. Strom (1991), 2. Bjornsen & Kuparinen 1991, 2. Hansen (1992), 3. Jacobson (1987) in Hansen (1992), 4. Scott (1985), 5. Ohman & Snyder (1991), 6. Verity (1985).

Protozoan taxa	Med GGE	Species	Food type & concentration	Ref
Dinoflagellates	0.23	*Gymondinium* sp.	Nf, Cy, Coc,	1
		Gyrodinium sp.	>0.4 μg Chl *a* L^{-1}	2
			Nf, Crypto,	
		Protoperidinium sp.	1-8 x 10^3 cells ml^{-1}	3
			Diatoms,	
			concn n.s.	
Ciliates	0.13	*Strombidium* sp.	Nf, 0.3 Joules ml^{-1}	4
			Bact,	5
			0.5–1.0 x 10^6 cells	
			ml^{-1}	
Tintinnids	0.33	*Tintinnopsis* spp.	Pr, 80-500 μg C L^{-1}	6

Gross growth efficiencies for copepods were calculated based on species-specific growth and ingestion rates (GGE = G/I). Growth rates were calculated using the exponential growth equation $G = \ln (W_t/W_0)/t$. W_0 is the initial stage dry weight, W_t is the final stage dry weight, and t the developmental time between stages. All copepods except *P. antarctica* occurred as copepodite stages during this study, therefore growth rates were determined from nauplius stage I to copepodite stage V. The population of *P. antarctica* consisted of mostly adult females, therefore a growth rate from copepodite stage V to copepodite stage VI was determined for this species. Dry weight and development times were determined from the literature (see Table 6.2). Ingestion rates of phytoplankton determined by Swadling et al. (1997) were used for all species except harpacticoids. The harpacticoids in

this study were much smaller (around 1 mm in length) than those reported in Swadling et al. (1997). Therefore, I used the dry weight for a small benthic harpacticoid species (measuring 0.75 mm in length) in Brown & Sibert (1977) and averaged the reported ingestion rates for this species feeding on algae and bacteria. In addition, ingestion rates of protozoa by *O. similis* during late summer (when protozoa were abundant) were determined by averaging the grazing rates of *O. similis* on protozoa in the Southern Ocean (Atkinson 1995, Lonsdale et al. 2000). To convert the data in Atkinson (1995), an average clearance rate of 2500 ml mg dry weight^{-1} d^{-1} for nano- and dinoflagellate prey was converted to an ingestion rate of 0.038 μg C ind^{-1} d^{-1}, using the reported measurements of copepod dry weight, and a carbon to chlorophyll *a* conversion of 50 for the Southern Ocean (Bjørnsen & Kuparinen 1991). An ingestion rate of 0.348 μg C ind^{-1} d^{-1} was calculated from the average clearance rate on non-loricate ciliates and ciliate cell carbon reported in Lonsdale et al. (2000). The overall GGE for copepods was determined as described for protozoa (see above).

Table 6.2. Data used to calculate copepod gross growth efficiencies for the four dominant species in Ellis Fjord. Note: the NI dry weight used for *O. curvata* and harpacticoids is that of NI *O. similis*, and harpacticoid data is based on the small harpacticoids in Kirkwood (1993) and *Drescheriella glacialis* in Bergmans et al. (1991). [1]Fransz & González (1995), [2]Kirkwood (1993), [3]Fransz (1988), [4]Bergmans et al. (1991), [5]Swadling & McKinnon (in prep).

Copepod taxa	W_0 (μg C)	W_t (μg C)	t (days)
Oithona similis	0.07 (NI)	1.9 (CV)[1]	220.0[1]
Oncaea curvata	0.07 (NI)	0.624 (CI-CV)[2]	183.0[3]
Harpacticoids	0.07 (NI)	0.416 (CI-CV)[2]	95.8[4]
Paralabidocera antarctica	19.69 (CV)	32.54 (CVI)[5]	10.0[5]

The flux of unidentified detrital material was obtained by subtracting the combined flux of protists and faecal pellets from the total measured POC flux. Re-working processes are not represented in the models.

6.3 Results

6.3.1 Water column biomass

6.3.1.1 Protists

Phytoplankton biomass was relatively low in the upper (0-10 m) water column during early summer, but increased rapidly in late January to a peak of 3421 mg C m^{-2} and generally declined thereafter during February (Figure 6.1a). This peak of phytoplankton biomass was largely due to nanoplanktonic taxa. The biomass of microplanktonic taxa remained relatively constant throughout the summer, with the exception of an increase in late February. The integrated phytoplankton biomass in the lower 10-40 m of the water column was slightly higher than that from 0-10 m (Figure 6.1b). While a temporal pattern in biomass was similar to that in the upper water column, the peak biomass of >4000 mg C m^{-2} occurred a week later in the lower water column, during early February, and the biomass of both micro- and nanoplanktonic taxa was more variable.

The biomass of protozoa was generally low throughout the water column during early summer (Figures 6.1c & d). However, a rapid increase was observed in the lower water column during early February reaching a concentration of 3676 mg C m^{-2}. A peak was observed one week later in the upper water column (Figure 6.1c). Protozoan biomass remained high throughout February. The contribution by nanoplanktonic protozoa was negligible and microplanktonic taxa comprised almost the entire protozoan biomass.

6.3.1.2 Copepods

Paralabidocera antarctica and *Oncaea curvata* dominated copepod biomass (Figure 6.2). The biomass of *P. antarctica* was highest in the upper water column during early January, though this species was absent from the lower water column at this time (Figure 6.2a). However, from late January to mid February, biomass was greater at lower depths (Figure 6.2b). The biomass of *O. curvata* was highest in early summer when this species occurred in both the upper and lower water column (Figures 6.2a & b), although *O. curvata* still contributed substantially to copepod biomass in the lower water column during late summer.

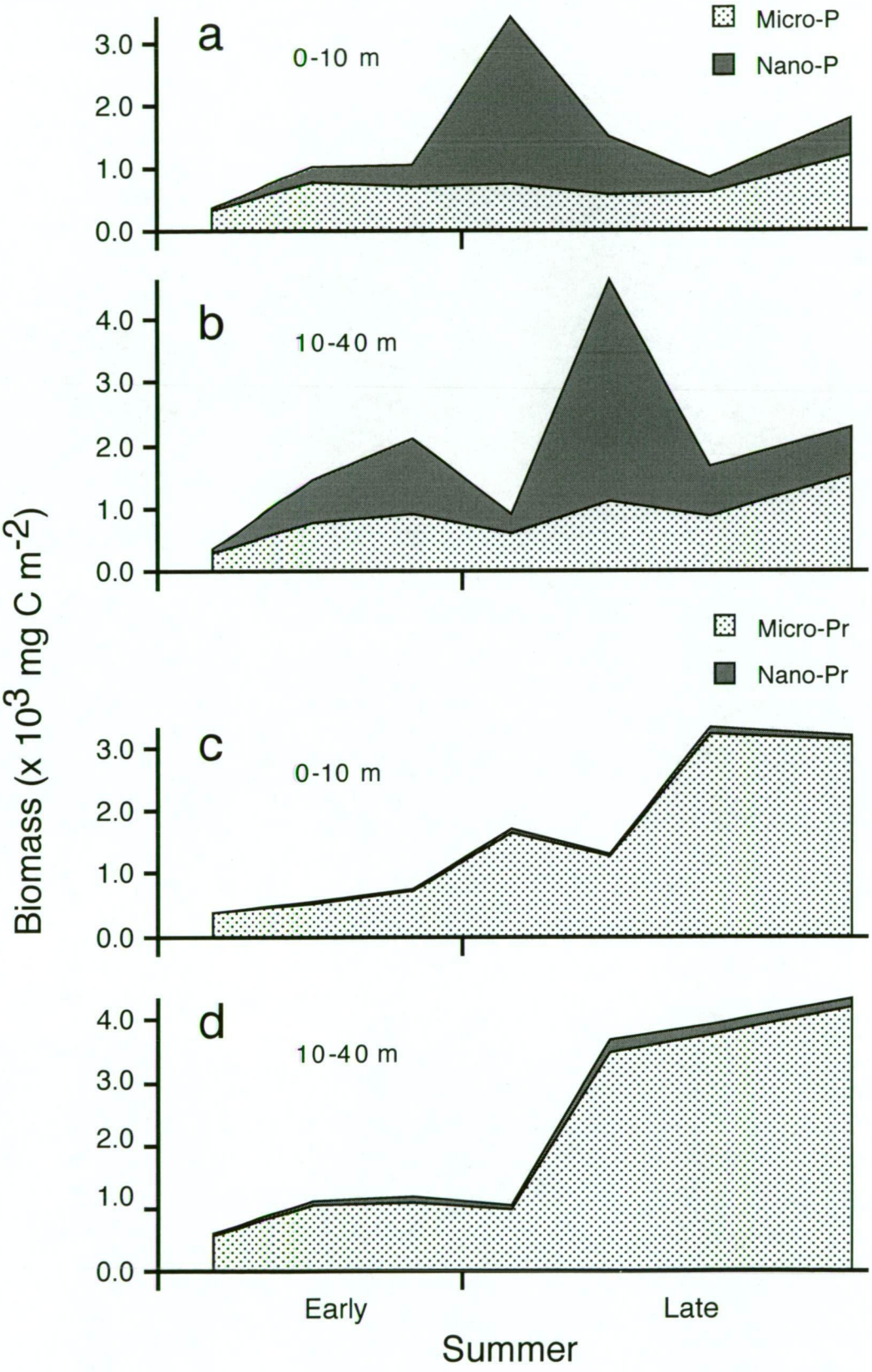


Figure 6.1. Protistan biomass during summer in Ellis Fjord. a & b) micro- and nanoplanktonic phytoplankton (Micro-P, Nano-P) in the upper (0-10 m) and lower (10-40 m) water column, respectively. c & d) micro- and nanoplanktonic protozoa (Micro-Pr, Nano-Pr) in the upper (0-10 m) and lower (10-40 m) water column, respectively.

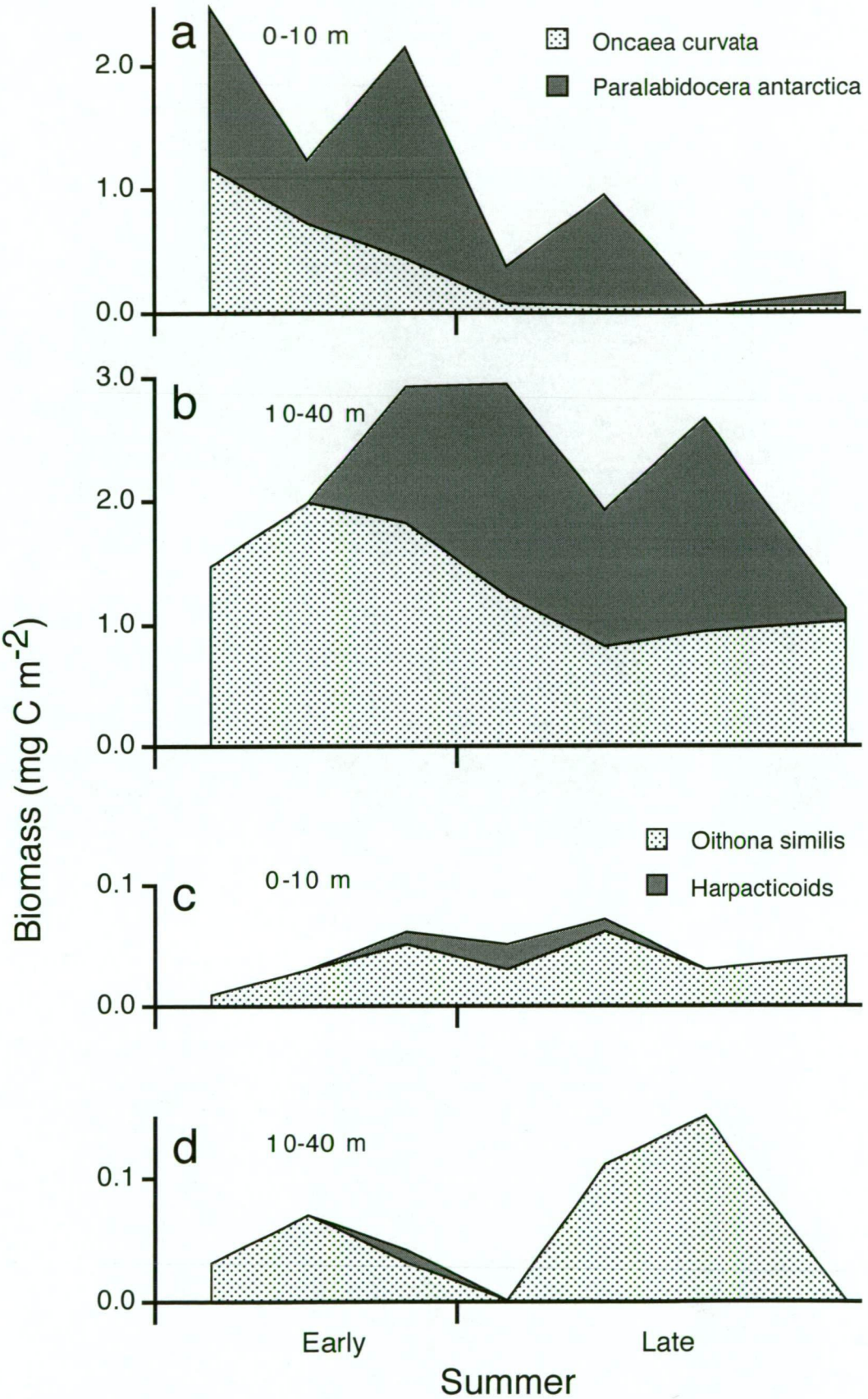


Figure 6.2. Copepod biomass during summer in Ellis Fjord. a & b) *Oncaea curvata* and *Paralabidocera antarctica* in the upper (0-10 m) and lower (10-40 m) water column, respectively. c & d) *Oithona similis* and harpacticoids in the upper (0-10 m) and lower (10-40 m) water column, respectively.

Overall, the biomass of *Oithona similis* and harpacticoids was low, reaching a maximum of <0.2 mg C m^{-2} during late summer. In the lower water column the biomass of harpacticoids was negligible, while that of *O. similis* was greatest during February.

6.3.2 Biogenic flux

6.3.2.1 Protists

Phytoplankton flux in the upper 0-10 m of the water column increased throughout January, reaching a peak of 6.83 mg C m^{-2} d^{-1} in early February, but declined rapidly thereafter (Figure 6.3a). The highest flux of phytoplankton occurred in the lower 10-40 m of the water column in early January (Figure 6.3b). However, this flux was an isolated occurrence and, with the exception of a small flux at the end of February, no further flux of phytoplankton was observed in the lower water column. Microplanktonic taxa dominated both phytoplankton and protozoan flux (Figure 6.3). A small flux of protozoa occurred in the upper 10 m of the water column during February, however, protozoan flux to depth was negligible (Figures 6.3c & d).

6.3.2.2 Faecal pellets

In upper waters, protozoan pellets were responsible for most of the carbon flux during early summer, as a result of their abundance and relatively high carbon content (Figure 6.4a, Table 6.3). However, during late summer oval pellets dominated carbon flux, reaching a peak of 7.50 mg C $m^{-2}d^{-1}$ (Figure 6.4c).

Cylindrical copepod pellets contained the most carbon per pellet, due to their generally larger volume than other pellet types (Table 6.3). Despite this, their contribution to carbon flux in upper waters was an order of magnitude lower than that of oval copepod pellets and large protozoan pellets (Figures 6.4a & c). While cylindrical pellets were the only pellet type that sank to depth, their contribution to vertical carbon flux was negligible (0.3 mg C $m^{-2}d^{-1}$) (Figure 6.4d). Similarly, minipellets were observed at depth, but due to their size and low carbon content, they also did not contribute to carbon flux to the lower water column (Figure 6.4b).

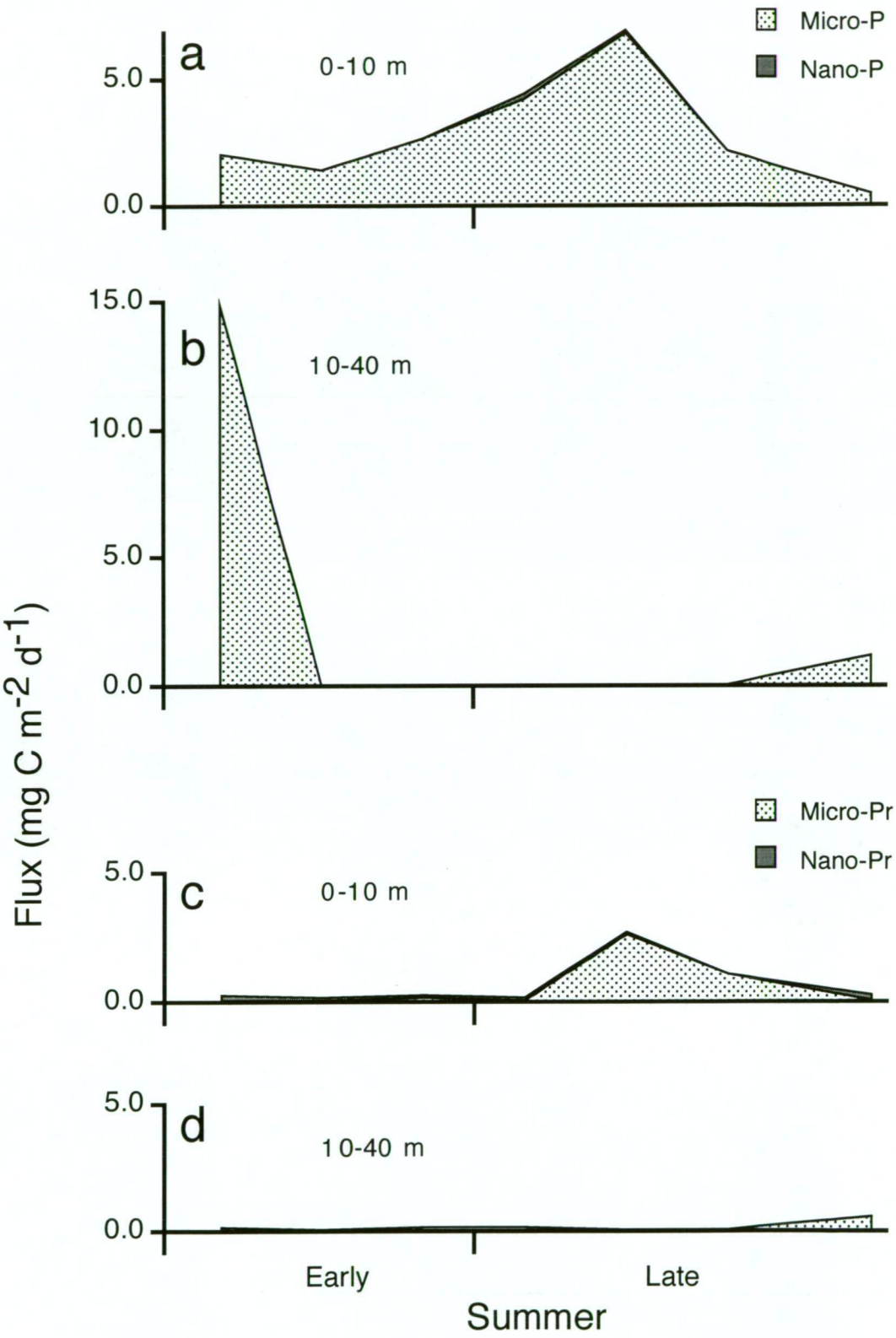


Figure 6.3. Protistan flux during summer in Ellis Fjord. a & b) micro- and nanoplanktonic phytoplankton (Micro-P, Nano-P) in the upper (0-10 m) and lower (10-40 m) water column, respectively. c & d) micro- and nanoplanktonic protozoa (Micro-Pr, Nano-Pr) in the upper (0-10 m) and lower (10-40 m) water column, respectively.

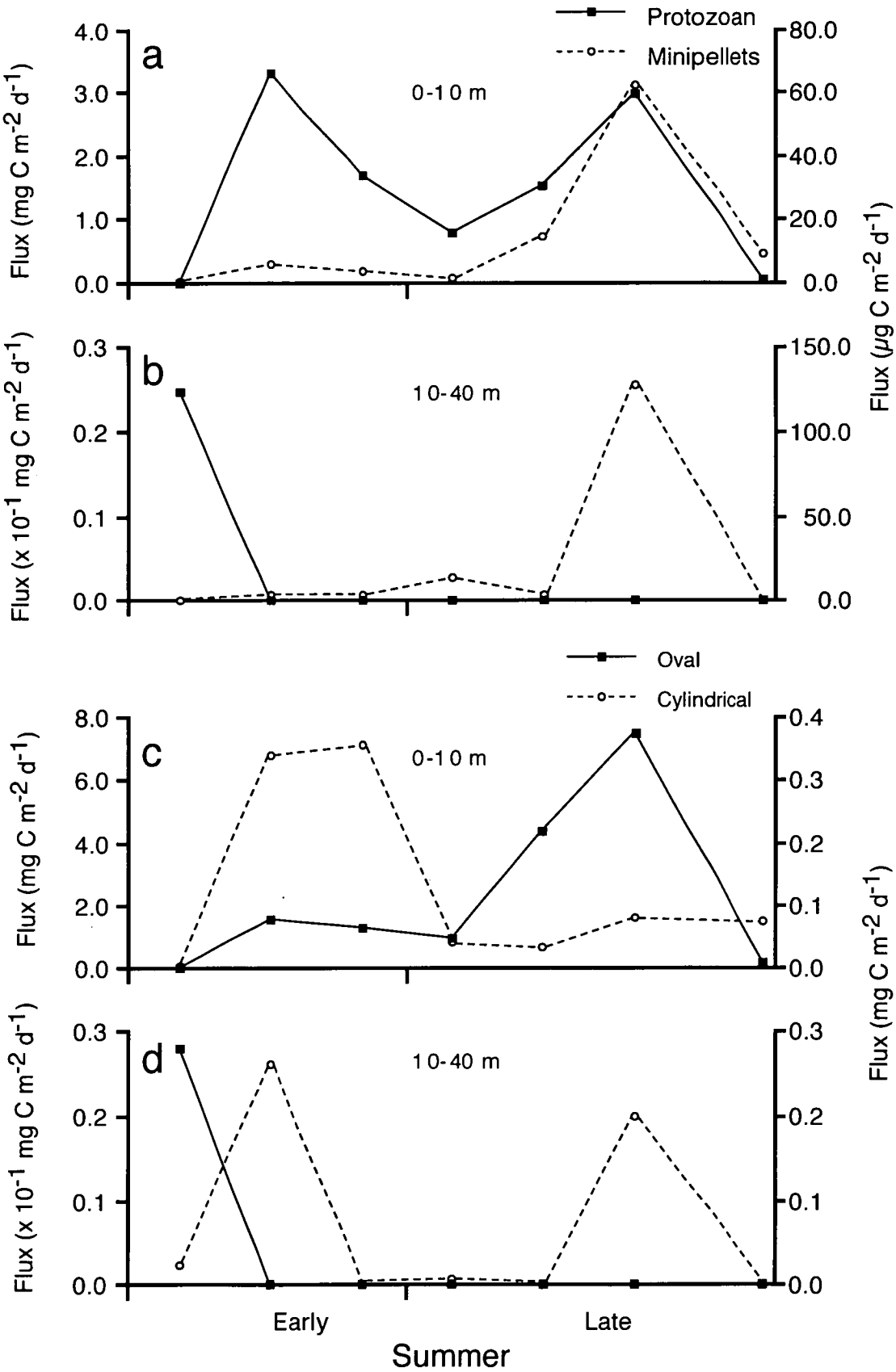


Figure 6.4. Faecal pellet flux during summer in Ellis Fjord. a & b) protozoan (left axis) and minipellets (right axis) in the upper (0-10 m) and lower (10-40 m) water column, respectively. c & d) oval (left axis) and cylindrical (right axis) copepod pellets in the upper (0-10 m) and lower (10-40 m) water column, respectively. Note the differences in scale.

Table 6.3. Measured and calculated faecal pellet carbon content. Minipellet types are: 1 oval consolidated, 2 spherical, 3 semi-transparent oval and irregular. [1]Urban-Rich 1997, * measured values (this study), ** back-calculated values (this study)

Pellet type	Conversion (pg C μm^{-3})	Average Vol (μm^{-3})	Concentration (μg C $pellet^{-1}$)
Cylinder	0.04 [1]	1.25×10^6	0.050
Oval	-	1.88×10^6	0.017*
Protozoan	-	1.79×10^7	0.026*
Minipellet 1	0.0091**	3.32×10^4	0.0003
Minipellet 2	0.0015**	1.80×10^5	0.0016
Minipellet 3	0.0015**	1.41×10^4	0.00002

6.3.2.3 Particulate organic carbon

The flux of POC in the upper water column was relatively low in early summer (< 100 mg C m^{-2} d^{-1}), but rapidly increased in late January to a peak of around 300 mg C m^{-2} d^{-1}. Thereafter, this flux declined prior to a slight increase at the end of February (Figure 6.5a). POC flux to lower waters was low (<30 mg C m^{-2} d^{-1}), occurring only once in early summer and again at the end of late summer (Figure 6.5b).

6.3.3 Primary production and grazing

Primary production was >1000 mg C m^{-2} d^{-1} during early summer, and further increased during late summer to more than 3000 mg C m^{-2} d^{-1} in the lower water column (Table 6.4). The percentage of primary production grazed by protozoa was substantially greater than that grazed by small copepods and increased from early to late summer, whereas that by small copepods decreased. In addition, both protozoan and copepod grazing was greatest in the upper water column during early summer. However, during late summer copepod grazing was lower in upper waters, while that by protozoa was generally uniform throughout the water column.

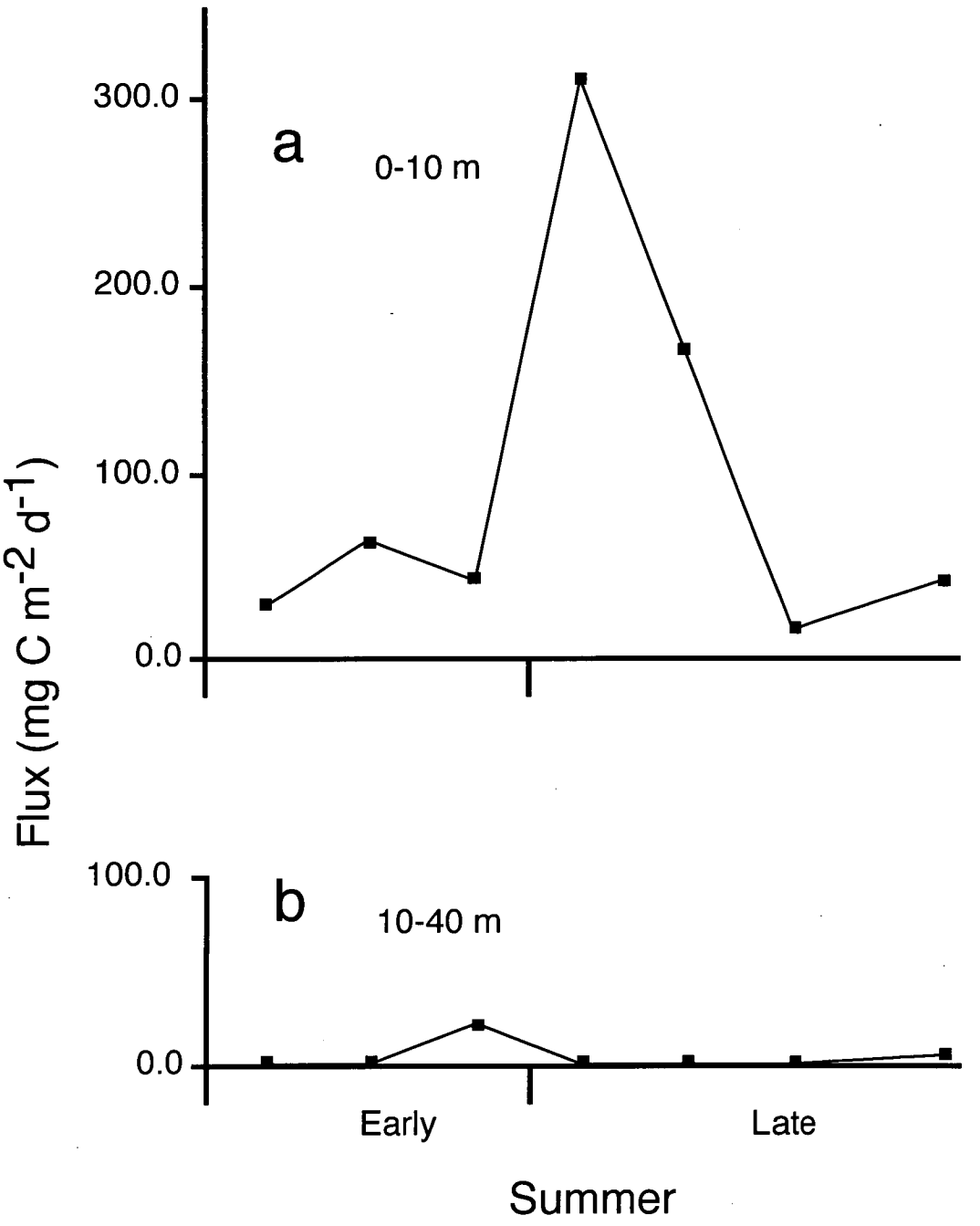


Figure 6.5. The flux of total particulate organic carbon during summer in Ellis Fjord in a) the upper 0-10 m of the water column, and b) the lower 10-40 m.

Table 6.4. Primary production and potential consumption by protozoa and small copepods in the upper 0-10 m and lower 10-40 m of the water column during summer in Ellis Fjord.

	Primary production	% Grazed	
	(mg C m^{-2} d^{-1})	Protozoa	Copepods
Early summer			
0-10 m	1087	310	17
10-40 m	1740	283	10
Late Summer			
0-10 m	2541	434	1
10-40 m	3194	410	5

6.3.4 Carbon flux models

6.3.4.1 Gross growth efficiencies

Gross growth efficiencies (GGE) varied between copepod species. Adult *Paralabidocera antarctica* had the lowest GGE while the highest GGE was that of *Oithona similis* copepodites feeding on heterotrophs (Table 6.5).

Table 6.5. Copepod gross growth efficiencies (GGEs) of the four dominant copepods in Ellis Fjord. [1]feeding on phytoplankton, [2]feeding on heterotrophs

Copepod species	GGE
Paralabidocera antarctica	0.008
Oncaea curvata	0.014
Harpacticoids	0.025
Oithona similis [1]	0.017
Oithona similis [2]	0.078

6.3.4.2 Early summer

Microplanktonic taxa dominated both the total phytoplankton and protozoan biomass in the upper water column (0-10 m). The total protozoan biomass was >70% that of the total phytoplankton biomass, requiring around four times the standing stock of phytoplankton to sustain protozoan stocks (Figure 6.6a). Copepod biomass was substantially lower than that of the protist community requiring <1/4 of the standing stock of protists to support the population. The direct flux of phytoplankton was low (<0.3%) and largely due to microplanktonic taxa. Total protozoan flux was negligible. However, the flux of large protozoan faecal pellets was considerable and exceeded that of copepod pellets. The flux of total POC was substantial and >80% of this flux was due to detritus.

Integrated phytoplankton and protozoan biomass was higher in the lower water column (10-40 m) than in upper waters (Figure 6.6b). However, while micro- and nanoplanktonic taxa contributed equally to the total biomass of phytoplankton, microplanktonic taxa comprised the majority of the protozoan biomass. The protozoan standing stock represented a greater proportion (around 3/4) of the phytoplankton stock than in upper waters, however, the carbon required to sustain the stock was slightly lower. Copepod biomass was similar to that in upper waters, requiring relatively little of the protist stock to sustain the population. The flux of phytoplankton was around twice the magnitude of that in upper waters and was also due to microplanktonic taxa. Total protozoan flux was negligible and no flux of protozoan or copepod faecal pellets was observed. Total POC flux was low and the contribution by the detritus pool to this flux was considerably lower than that in upper waters.

6.3.4.3 Late summer

Nanoplanktonic taxa dominated the phytoplankton biomass in the upper water column while the protozoan biomass remained dominated by microplanktonic taxa (Figure 6.6c). The carbon requirement to sustain the protozoan biomass was >5 times the standing stock of phytoplankton. Copepod biomass was extremely low and required <0.2% of the phytoplankton biomass to maintain the population. The fluxes of phytoplankton and protozoa were dominated by microplanktonic taxa, and

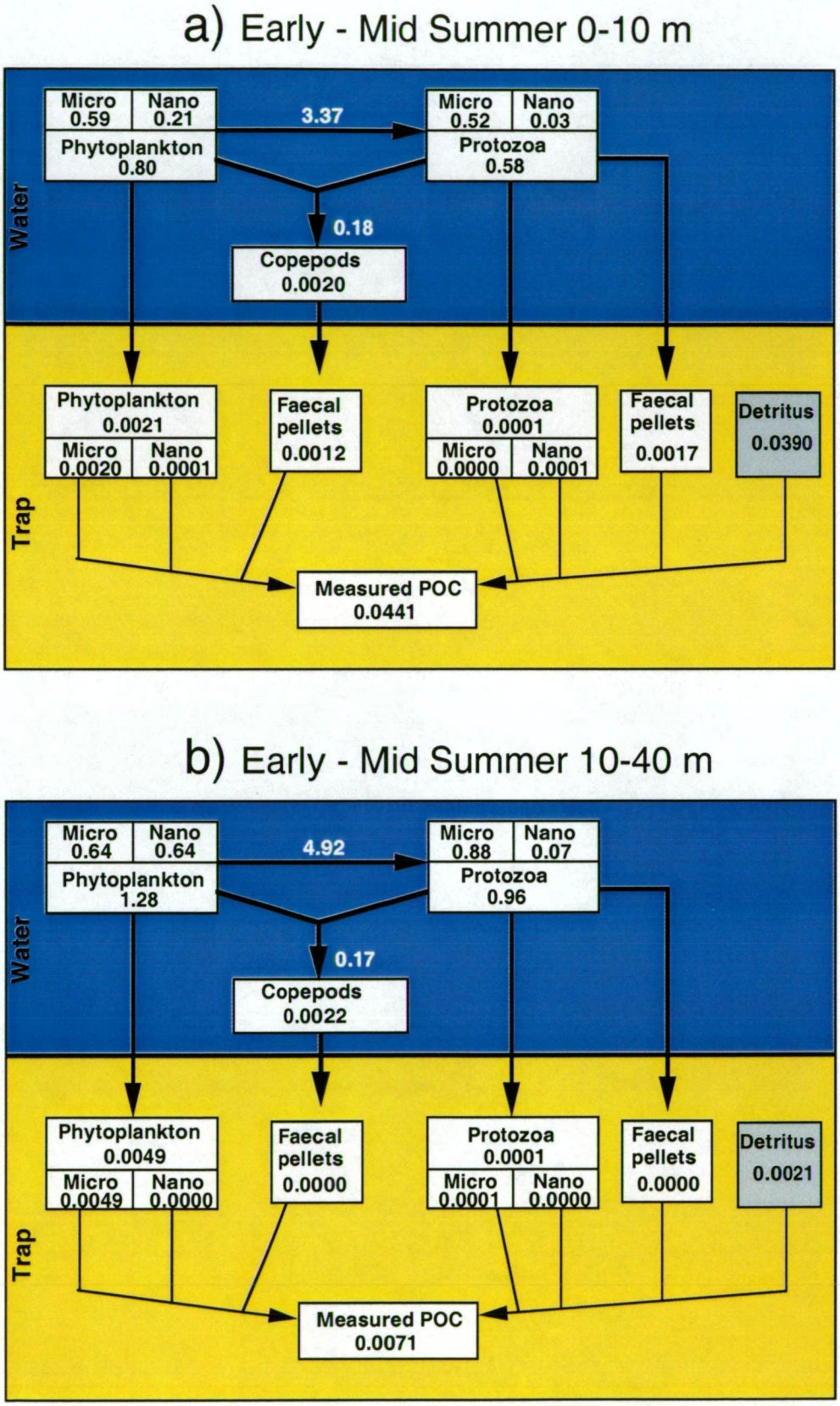


Figure 6.6. Biomass (g C m^{-2}) in the upper and lower water column and daily flux to traps (g C m^{-2} d^{-1}) in Ellis Fjord during a-b) early summer, and c-d) late summer. Numbers outside boxes represent consumption.

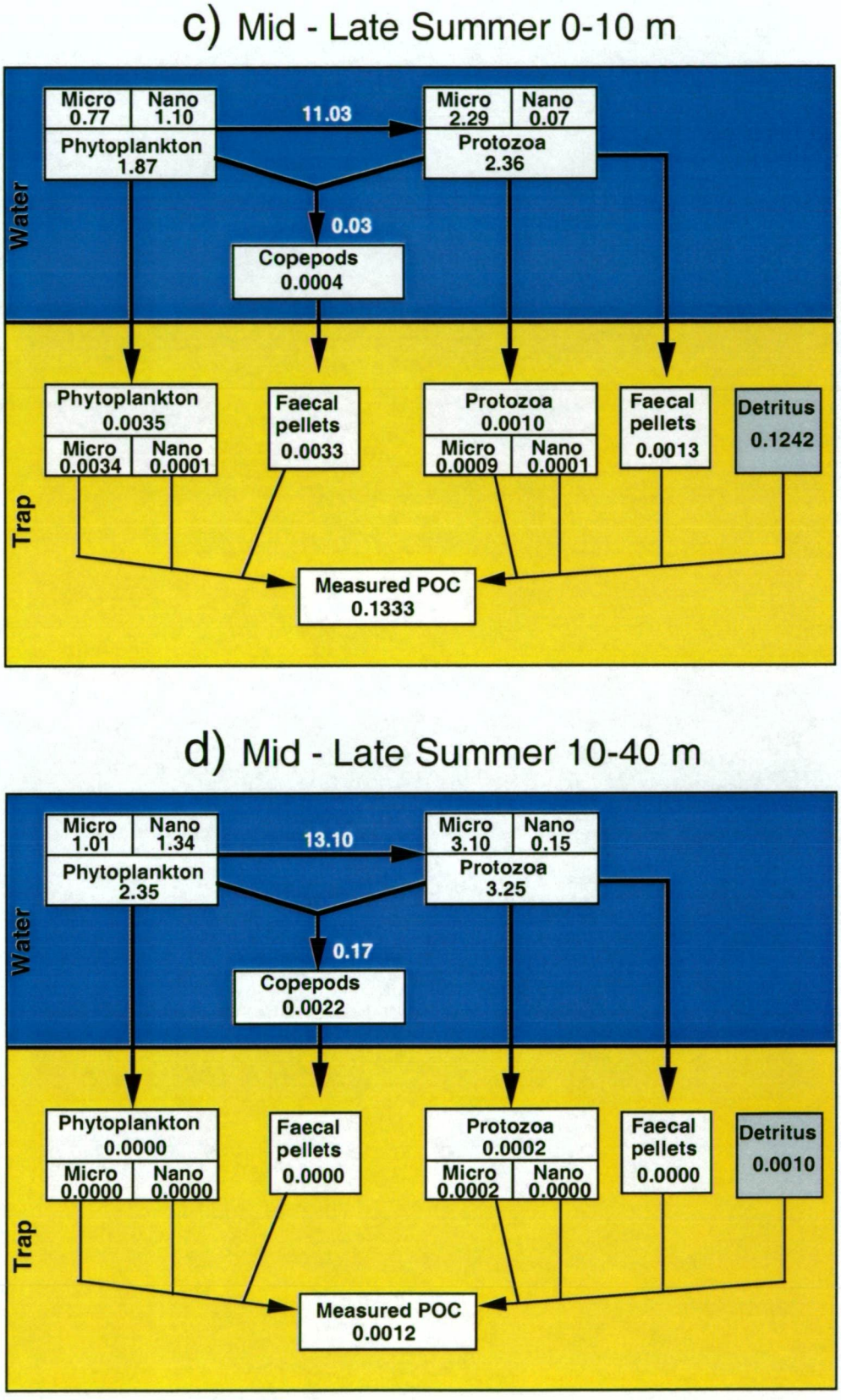


Figure 6.6. Biomass (g C m^{-2}) in the upper and lower water column and daily flux to traps (g C m^{-2} d^{-1}) in Ellis Fjord during a-b) early summer, and c-d) late summer. Numbers outside boxes represent consumption.

together made a notable contribution to carbon flux. The flux of large protozoan faecal pellets was approximately half that of the copepod pellets. The flux of copepod pellets and total POC was the highest recorded throughout the entire summer and detritus comprised the majority of the POC flux.

Micro- and nanoplanktonic taxa contributed almost equally to the total phytoplankton stock in the lower water column, while protozoan biomass was again dominated by microplanktonic taxa (Figure 6.6d). Similar to upper waters, >5 times the phytoplankton standing stock was required to support the protozoan biomass. While copepod biomass was higher than that in upper waters, it remained relatively low and only required around 7% of the protist stock to sustain the population. No flux of phytoplankton was observed, and there was only a minor flux of microplanktonic protozoa. In addition, no fluxes of either protozoan or copepod faecal pellets were observed, and the flux of total POC was the lowest recorded throughout the summer, and comprised mostly detritus.

6.4 Discussion

The biomass in Antarctic waters is dominated by marine microbes and microzooplankton. These organisms respire much of the primary production, and contribute to a web of complex trophodynamics that support higher trophic levels. However, their role in vertical carbon flux is poorly understood. Models of carbon flux in the Southern Ocean have generally used broad taxonomic groups to examine the biogenic fluxes through marine communities. Yet, it is increasingly recognised that the ecology of individual species is highly complex and, consequently, the trophic roles of different taxa can overlap (Sanders & Wickham 1993, Wickham 1995, Granéli & Turner 2002). My study has developed models of carbon fluxes based on species-specific ecologies and interactions to provide the fine-scale resolution required for community models to be realistic (Paffenhöfer 1998). These models include the first measurements of faecal pellet carbon for protozoan pellets, and the calculation of species and taxa-specific gross growth efficiencies (GGEs). The determination and justification of the variables used to develop the models is presented prior to discussion of the modelled plankton dynamics.

6.4.1 Data justification

6.4.1.1 Protists

Changes in the biomass of individual taxa affect the direct sedimentation of protist carbon and also the carbon transfer to the grazer community (see Chapters 3 & 5). With few exceptions, studies investigating protist biomass in relation to carbon flux have used broad-scale techniques such as size-fractionated primary production and chlorophyll *a*, that provide little information on the taxonomic composition of the protistan biomass (e.g. Wefer & Fischer 1991, Villafane et al. 1993, Fiala et al. 1998, Kelley et al. 1999). To examine the regulation of the protistan carbon flux, I undertook detailed microscopic analysis and calculated cell volumes of individual genera. I did not account for the effect of fixative on cell volume and this may have have led to the over-estimation of protist carbon based on cell volume. However, while equations have been established to correct for the effects of fixation on the cell volumes of group taxa, estimating changes in individual genera is highly complex and at present remains unresolved in the literature (Menden-Deuer et al. 2001).

6.4.1.2 Primary production

The calculated gross primary production in my study was high for an under-ice community. These calculations were based on $^{14}CO_3^{2-}$ incubations of up to 4 hours (Swadling et al. 1997), and represent an integrated estimate of production based on phytoplankton biomass in the water column. This does not account for changes in the physical environment with depth or time that may influence community production. However, to my knowledge, there are no reports in the literature of the vertical distribution of primary production under fast-ice. While primary production may have been over-estimated in my study, similarly high rates have been recorded in relatively sheltered coastal waters in the Antarctic (Holm-Hansen & Mitchell 1991, Saggiomo et al. 1998, Saggiomo et al. 2002), and low turbulence reportedly leads to high rates of production that result in large phytoplankton blooms. In Ellis Fjord, the ice-cover, limited turbulent mixing, and photoadaptation of phytoplankton to under-ice irradiance can result in high phytoplankton

standing stocks, and apparently high primary production (Gibson 1998, this study).

6.4.1.3 Faecal pellets

The determination of total faecal pellet carbon was largely based on carbon measurements of individual pellet types. Measured carbon concentrations in this study, and those reported in the literature, varied considerably between pellet types. The carbon concentration I measured for oval copepod pellets of 0.009 pg C μm^{-3} was similar to the lowest reported concentration of 0.01 pg C μm^{-3} for pellets from >500 μm mesozooplankton (Urban-Rich 1997), but substantially lower than the 0.061–0.069 pg C μm^{-3} reported for large calanoid copepod pellets from polar waters (Wassmann et al. 1999, Reigstad et al. 2000). Such measurements, together with carbon to dry weight and carbon to volume conversions, are often extrapolated to all pellet types to determine the relative contribution by faecal pellets to flux (e.g. Small et al. 1987, Lane et al. 1994, Carroll et al. 1998, Reigstad et al. 2000). My results show that the volume-specific carbon content of faecal pellets produced by small copepods represents around 1/7 that of large copepods. Therefore, studies that use generic carbon to volume conversions may severely over-estimate the contribution by faecal pellets to carbon flux (Urban-Rich et al. 1998). Furthermore, such conversion factors do not account for seasonal changes in faecal pellet carbon due to changes in food quality and quantity (Urban-Rich et al. 1998, Pasternak et al. 2000, Urban-Rich 2001). In this study, faecal pellets of each type were pooled over the season for CHN analysis. Thus, the measured carbon content of pellets encompassed any temporal variation.

My results show that the carbon content of large protozoan pellets appears to be lower than previously thought. Concentrations have previously been estimated using the cytoplasmic content of cells within an average-sized pellet or the phytoplankton plasma conversion determined by Strathmann (1967) (Bathmann et al. 1987, Buck et al. 1990, González et al. 1994b, Buck & Newton 1995). Such estimations are considered to over-estimate pellet carbon, as the majority of phytoplankton cells within the pellets are devoid of cell contents (Buck & Newton 1995). The volume-specific conversion I obtained from the CHN analysis of over 300 pellets was 1/50th (0.001 pg C

μm^{-3}) of that obtained by the aforementioned methods in the literature. Therefore, studies that have used these inflated values will have severely overestimated the contribution by protozoa to carbon flux (Klaas 1997b, Gowing et al. 2001).

It may have been predicted that large protozoan pellets would contain relatively little carbon, due to the absence of phytoplankton cell contents. Despite the relatively low carbon content of this pellet type, the carbon concentration per pellet exceeded that of oval copepod pellets, suggesting that the mucoid membrane surrounding protozoan pellets must be relatively carbon-rich.

6.4.1.4 Gross growth efficiencies

Gross growth efficiencies (GGEs) were calculated to quantify the energy required to sustain the biomass of protozoa and copepods. Unlike net growth efficiencies (NGEs), GGEs may over-estimate the requirements for growth as they do not account for the non-assimilation and excretion of energy ingested. However, to determine NGEs requires knowledge of faecal pellet production rates and these could not be determined accurately from field data, due to the spatial and temporal uncoupling of the abundance of faecal pellets and their producers. Furthermore, I am not aware of any reports in the literature of pellet production rates for the copepod species in this study, nor for protozoa in general.

Copepods

Gross growth efficiencies are influenced by food quality and concentration and, to a much lesser extent, temperature. To determine energy transfers realistically, models should incorporate detailed, site-specific information (Vézina & Platt 1988). Global growth equations for marine planktonic copepods have been established that attempt to account for temperature and species metabolism (Hirst & Lampitt 1998, Ikeda et al. 2001). However, the equations established by Hirst & Lampitt (1998) are mostly based on data from broadcast spawners and do not include data from small copepods, and the equations by Ikeda et al. (2001) have inherent problems for regional sites with low copepod diversity (Huntley & Lopez 1992, Ikeda et al. 2001). Consequently, exponential growth rate equations were used for small

copepods in this study, as they rely on specific life-stage data and thereby account for ontogenetic changes in GGEs that occur during copepod development (Paffenhöfer 1976, Omori & Ikeda 1984, Swadling & McKinnon in prep). While exponential growth equations do not account for changes in temperature, studies that have examined temperature dependency of growth found changes at intervals of ≥5 °C (Hirst & Lampitt 1998). Temperature changes at my study site during summer are reportedly ≤1°C (Gibson 1999).

The GGEs used in this study were determined from copepod species-specific ingestion rates and dry weights from the study region, and development times from the Southern Ocean, and are therefore robust as they account for both species and site-specific characteristics (Vézina & Platt 1988, Paffenhöfer 1993).

Protozoa

Most studies in Antarctic waters have used a fixed GGE of 0.3-0.4 for protozoans to calculate either growth or ingestion rates (e.g. Bjørnsen & Kuparinen 1991, Garrison 1991, Archer et al. 1996a, Klaas 1997b). However, similar to Straile (1997), I suggest these GGEs used in Antarctic studies have possibly been applied uncritically as the GGE has often been assumed (Garrison 1991, Klaas 1997b), or extrapolated within protozoan taxa (e.g. from flagellates to dinoflagellates) that have different food preferences and feeding rates (Bjørnsen & Kuparinen 1991). It has been demonstrated that changes in food quality and quantity can substantially affect the GGE and that the general assumption of 0.4 for protozoans may severely underestimate protozoan grazing, particularly during blooms, as it is well established that GGEs and assimilation efficiencies are low when food is abundant, due to incomplete digestion (Straile 1997). Therefore, the quality and quantity of available food should be considered when determining planktonic GGEs in models of carbon flux (Caron et al. 1990, Straile 1997).

I used a GGE of 0.3 for heterotrophic nanoflagellates (HNF) that was measured for HNF feeding on bacterioplankton in the Southern Ocean (Lancelot et al. 1997). For microprotozoan taxa in Ellis Fjord, I obtained genera-specific GGEs of protozoa feeding on cryptophytes, diatoms and other auto- and heterotrophic protists of similar concentration to that observed at my study site (Table 6.1). These genera-specific GGEs (0.13-0.33)

were lower than the value of 0.4 previously adopted in studies of plankton energetics in Antarctic waters (see above), but within the range of GGEs reported for protozoa by Straile (1997).

6.4.2 Plankton biomass

6.4.2.1 Protists

The biomass of microphytoplankton remained relatively low and constant throughout the summer at <1.0 g C m^{-2}, while blooms of nanoplankton (primarily cryptophytes) led to the total phytoplankton biomass during late summer reaching up to 3.4 and 4.6 g C m^{-2} in the upper and lower water column, respectively. Gibson (1998) reported similar blooms of cryptophytes of 3.75 g C m^{-2} in an integrated water column during a previous summer in Ellis Fjord. Cryptophtyes can reportedly dominate phytoplankton biomass in Antarctic coastal waters during summer ranging from 1.2 - 3 g C m^{-2} (Nöthig et al. 1991, Kang & Lee 1995). However, in general, blooms of microplanktonic diatoms dominate phytoplankton biomass in the Southern Ocean (Villafane et al. 1993, Kang & Lee 1995, Moline et al. 1997, Socal et al. 1997). The relatively low biomass of the diatom bloom in the present study may have resulted from, amongst other environmental factors, the limitation of available silica (McMinn et al. 1995), or may have been due to the high biomass of protozoan grazers (see below).

The protozoan biomass, was relatively low in early summer (<1.0 g C m^{-2}), but reached 3.25 g C m^{-2} during late summer. Similar to findings of previous studies, microplanktonic taxa, namely dinoflagellates and ciliates, dominated the protozoan biomass (Garrison 1991, Garrison & Gowing 1993). The lower biomass observed during early summer is comparable with maximum values reported in other studies, while that in late summer is high (c.f. Garrison & Gowing 1993 and references therein). Such high stocks (>2.0 g C m^{-2}) have only been reported by Nöthig (1988) in the Eastern Weddell Sea. The shallow, mixed layer, resulting from summer warming and ice-melt, fosters development of blooms of protists (Smith & Nelson 1986, Kottmeier & Sullivan 1987, Lancelot et al. 1993, Carrada et al. 2000). During my study, this coincided with a bloom of cryptophytes that appeared to promote rapid growth of protozoa, resulting in protozoan carbon representing more than half (58%) of the total protistan carbon. Similarly,

Nöthig et al. (1991) found protozoa comprised a high proportion (49%) of protozoan to total protistan carbon in association with a surface melt-water layer in the Weddell Sea, and suggested that the increased stability of the water column allowed the development of substantial phytoplankton and heterotrophic biomass.

High standing stocks of protozoa have generally been reported in oceanic waters and the marginal ice zone (MIZ), with lower protozoan standing stocks occurring in ice-covered regions adjacent to the coast (Alder & Boltovskoy 1993, Burkill et al. 1995, Klaas 1997b). However, exceptions seem to appear where considerable algal blooms have occurred (Becquevort et al. 2000). Gibson (1998) reported that substantial phytoplankton blooms occur under the ice due to limited turbulent mixing and photoadaptation of phytoplankton to under-ice irradiance. My study shows that substantial protozoan stocks can also occur under the ice. In Ellis Fjord, the stability of the water column and an abundance of available food led to substantial heterotrophy and, perhaps, the highest protozoan biomass that has ever been reported in Antarctic waters.

6.4.2.2 Copepods

The biomass of the four dominant small copepods in Ellis Fjord was lower than that previously reported in the fjord by Kirkwood (1993), at an adjacent coastal site (Swadling 1998), and in general for the Southern Ocean (Fransz 1988, Atkinson 1998, Ward & Shreeve 1999). Similarly low copepod biomass has been reported in only a few studies from the adjacent coast (Tucker & Burton 1990), under ice-cover off Syowa station (Tanimura et al. 1986), and in coastal waters of the eastern Weddell Sea (Schnack-Schiel et al. 1998b). The biomass of copepods is variable but appears to be inversely related to protozoan biomass. Low biomass of small copepods coinciding with high protozoan biomass was also observed in the eastern Weddell Sea (Nöthig 1988, Schnack-Schiel et al. 1998b). Further, the opposite has also been reported from waters adjacent to Ellis Fjord; small copepod biomass was high and that of protozoa was low (Archer et al. 1996a, Swadling 1998).

The inverse relationship between the relative abundance of copepods and protozoa may be due to both physical and biotic factors. During my study in

Ellis Fjord, and Nöthig's (1988) in the Weddell Sea, sea ice melt stabilised the water column and promoted the development of phytoplankton blooms in upper waters. In Ellis Fjord it is likely that predation of small copepods by ctenophores, nototheniid fish fry, and possibly protozoa, limited copepod biomass (see Chapter 3). In contrast to the results of Swadling (1998) and Kirkwood (1993), large copepods, including *Calanoides acutus*, were largely absent. Such copepods can reduce the biomass of large (100-200 μm) ciliates and other protozoa (Atkinson 1995, Turner & Granéli 1992, Levinsen et al. 2000) while small copepods reportedly have a negligible effect on protozoan biomass (Lonsdale et al. 2000). In addition, the content of copepod and protozoan faecal pellets indicates that they graze the same phytoplankton taxa (Chapter 4). Thus, the composition of the copepod community and the limitation of their biomass by predation may have released protozoa and phytoplankton from top-down control by copepod grazing, leading to an increase in the biomass of these protists during my study. Further study is required to examine quantitatively the apparently reciprocal relationship between small copepods and protozoa, and its influence on vertical carbon flux.

6.4.3 Primary production and grazing

Primary production was high, ranging from 1087-3194 mg C m^{-2} d^{-1} throughout summer, and may have been over-estimated (see 6.4.1 Data justification). However, maximum rates of primary production recorded during summer in broken pack-ice off Terra Nova Bay, the MIZ in the Weddell Sea, and in open water in the Bransfield Strait, are of similar magnitude (Holm-Hansen & Mitchell 1991, Mathot et al. 1992, Saggiomo et al. 1998, Saggiomo et al. 2002). The rate of primary production reflects the distribution of phytoplankton biomass with depth and time, and the depth over which the biomass was integrated (see 6.4.1 Data justification). Therefore, production was generally higher in the lower water column due to the greater depth interval over which production was integrated, and increased during late summer due to the peak in phytoplankton biomass.

Protozoa grazed between 283 and 434% of the daily primary production. This is possibly the highest rate of consumption ever estimated in Antarctic waters, exceeding that of 271% previously reported in the Bellingshausen

Sea (Burkill et al. 1995). It has been increasingly reported that protozoan grazing of primary production can be >100% during summer in the Southern Ocean, and can thereby control phytoplankton production and contribute to reduced phytoplankton biomass (Becquevort et al. 1992, Lancelot et al. 1993, Tsuda & Kawaguchi 1997). The phytoplankton biomass in Ellis Fjord was maintained and increased during early summer, while during late summer protozoan grazing appeared to rapidly terminate the cryptophyte bloom. While phytoplankton contributed substantially to the diet of protozoa (see Chapter 4), protozoan grazing exceeded primary production throughout summer, suggesting that other food sources, such as ice-algae and bacterioplankton, were also utilized.

Ice-algae are an important source of primary production (Palmisano & Sullivan 1983) and were observed in the water column (see above). Bacterioplankton can also contribute substantially to the diet of protozoa (Garrison & Buck 1989, Becquevort et al. 1992, Delille et al. 2002). In addition, the extent to which protozoa feed on copepod eggs and nauplii is currently unknown, but these organisms may also be a source of nutrition (Sanders & Wickham 1993, Jeong 1994). The discrepancy between the phytoplankton standing stocks and the nutrition required to support the observed protozoan biomass in my study could have resulted from: the non-quantification of the aforementioned food sources; the indirect determination of protozoan grazing (based on the biomass and GGE) that does not account for changes in grazing rates in relation to the vertical light climate through the water column and the vertical migration of protozoa; and the inclusion of mixotrophic species in the determination of protozoan biomass. Therefore, protozoan grazing could have been over-estimated in this study. However, in the most extreme scenario that the actual grazing was less than half of that estimated in this study, protozoan grazing would still exceed primary production.

The GGEs used in this study to determine the magnitude of copepod grazing are robust as they are based on species and life-stage specific growth and ingestion rates (see 6.4.1 Data justification). These GGEs are around $1/45^{th}$ of those reported for large Antarctic copepods. However, they are comparable to GGEs reported by Gerber & Gerber (1979) for small tropical copepods. It is well established that a low GGE is due to incomplete digestion and low

assimilation efficiency when food is abundant (Straile 1997). My GGEs indicate that biomass specific grazing by the small copepod species in Ellis Fjord was some 45 times higher than that reported for large copepod species. While frequently dominating the carbon biomass in Antarctic waters, it has been reported that large copepods consume <1% of the primary production at the Antarctic Polar Front, but small copepods could graze >100% of the daily production (Dubischar et al. 2002). Similarly, Morales et al. (1993) and Swadling et al. (1997) report that small copepods exert more grazing pressure than large copepods, due to higher ingestion rates and abundances.

As noted above, copepod biomass in Ellis Fjord during early summer was lower than previously reported. Despite this low biomass, they were responsible for grazing 10-17% of the primary production. Copepods reportedly graze up to 56% of primary production in the Southern Ocean, but commonly graze < 10% (Schnack et al. 1985, Hopkins 1987, Atkinson & Shreeve 1995, Dubischar & Bathmann 1997, Razouls et al. 1998, Urban-Rich et al. 2001). However, such reports strongly reflect dominance of the copepod biomass by large species. If the biomass of small copepods in this study was increased to concentrations commonly reported for Antarctic coastal waters (e.g. Fransz 1988, Swadling 1998, Ward & Shreeve 1999), similar to Dubischar et al. (2002), they would graze >100% of the phytoplankton production. Thus it is likely that small copepods can limit the standing stocks of phytoplankton in Antarctic coastal waters.

During late summer, small copepods only grazed 1-5% of primary production. This reduction in grazing of phytoplankton may be due to increased concentrations of the omnivorous copepod *Oithona similis*, while concentrations of predominantly herbivorous species declined. This reduced grazing by small copepods during late summer may have resulted, at least in part, in the observed increases in phytoplankton biomass.

Though small copepods were responsible for substantial grazing of phytoplankton in Ellis Fjord, the biomass and grazing by microzooplankton throughout the summer was dominated by protozoa. Despite these differences in biomass and grazing pressure, these microzooplankton appear to be equal contributors to biogenic carbon flux (see below).

6.4.4 Biogenic flux

The only flux of phytoplankton to depth of 15 mg C m^{-2} d^{-1} occurred briefly at the beginning of January and was due to sedimenting ice-algae (see Chapter 5). While this was relatively low compared to ice-algal flux previously reported in Ellis Fjord (McMinn 1996), ice-algal biomass is reportedly highly patchy and variable between seasons (see Chapter 3). This flux of ice-algae represented 9.8% of the average ice-algal standing stock recorded in December (see Chapter 3), and 1.2% of the microplanktonic phytoplankton stock in the water column during January. Similarly, Cadée (1992) reported the flux of chlorophyll *a* during ice retreat in the Scotia-Weddell Sea ranged between 0.1 and 2.6% of the total planktonic standing stock, and Nöthig (1988) and Asper & Smith (1999) reported particulate fluxes of 0.6% and 2.3% of their standing stocks in the Weddell and Ross Seas, respectively. Despite this relatively low flux of phytoplankton carbon (average of 4.9 mg C m^{-2} d^{-1}) compared to the standing stocks, this constituted 69% of the daily POC flux during early summer. While a similar magnitude of flux has been reported in the Ross Sea polynya, the contribution to total POC was much lower, due to the large contribution by faecal pellets in this region (Gowing et al. 2001).

Direct flux of protozoa did not contribute to vertical carbon flux and the only minor contribution observed in the upper water column occurred when the phytoplankton bloom declined. Microplanktonic protozoa reportedly colonise phytoplankton aggregates (e.g. Silver et al. 1978, Michaels & Silver 1988, Silver & Gowing 1991, Azam 1998). Thus, flux of protozoa in the upper water column may have been due to sinking aggregates that had formed from the senescent phytoplankton bloom.

Faecal pellets did not contribute to carbon flux to depth, and the flux in upper waters was relatively minor, representing 7 and 3% of the total POC during early and late summer, respectively. This contrasts with other studies that report substantial fluxes of faecal pellets representing up to 90% of total POC (von Bodungen 1986, von Bodungen et al. 1987, Lutter et al. 1989, Cadée 1992, Andreassen et al. 1996). However, the majority of this flux was usually due to large krill pellets, and it has been increasingly reported that copepod pellets do not contribute substantially to flux in polar waters

(Peinert et al. 1982, Smetacek et al. 1990, Urban-Rich et al. 1999, Viitasalo et al. 1999, Dubischar et al. 2002). The only notable flux of faecal pellets in upper waters was dominated by oval copepod pellets and large protozoan pellets. The carbon flux of cylindrical copepod pellets and minipellets was negligible. While protozoan and minipellets can reportedly contribute to carbon flux to depth (Nöthig & von Bodungen 1989, Buck, et al. 1990, Bathmann et al. 1991, Gowing et al. 2001, Walsh et al. 2001), such observations may be due to an over-estimation of the carbon content of pellets (see 6.4.1 Data justification) and/or misidentification (see Chapter 4).

The fluxes of POC measured in Ellis Fjord during this study are similar to the range of fluxes reported in other Antarctic waters (Karl et al. 1991 and references therein). However, the consistently low export of POC to depth (<10 mg C m^{-2} d^{-1}) is similar to annual averaged fluxes in regenerative systems that occur throughout much of the year in Antarctic waters (Smetacek et al. 1990, Karl et al. 1991). High fluxes of POC to deep waters are generally episodic and result from either direct sedimentation or grazing of the spring / summer blooms (Karl et al. 1996, Le Fèvre et al. 1998, Turner 2002). While I observed a peak flux of 300 mg C m^{-2} d^{-1} in the upper 10 m of the water column during a cryptophyte bloom, the peak was brief and was not exported to depth as the community was dominated by microheterotrophic grazing (see 6.4.5 Carbon flux models below).

6.4.5 Carbon flux models

Despite a shift from an autotrophic microplanktonic based food web in early summer to one dominated by heterotrophic nanoplankton later in the season, most biogenic carbon was retained in the upper 10 m of the water column. The only exception was a brief and relatively minor flux of carbon derived from sinking ice-algae. This contrasts with the general view that a food web based on large phytoplankton will lead to the export of primary production, while a microbially based food web dominated by nanoplankton favours the retention of production in pelagic waters (Bienfang & Ziemann 1992, Bathmann 1996, Froneman & Perissinotto 1996). The retention of microphytoplankonic carbon in upper waters during early summer appeared largely due to the interaction between the physiological state of the diatom bloom (see Chapter 5) and grazing by protozoa and small copepods.

Actively growing cells have low sinking rates and persist in upper waters (Smayda 1970, Smetacek 1985, von Bodungen et al. 1986, Moline et al. 2000), while grazing can reportedly reduce the flux of phytoplankton to depth (Peinert et al. 1989, Pesant et al. 1998, Wassmann 1998).

It is becoming increasingly recognized that protozoan grazing can substantially reduce phytoplankton biomass and production (Garrison & Buck 1989, Burkill et al. 1995, Archer et al. 1996a, Klaas 1997a,b, Becquevort et al. 2000). Similar to these studies, the current study indicated that protozoan grazing was principally responsible for limiting phytoplankton production, while the impact of copepod grazing was relatively minor. This dominance of protozoan grazing was reflected by carbon from protozoan pellets occasionally exceeding that of copepod pellets in upper waters. However, in contrast to the model of carbon dynamics in the Southern Ocean developed by Walsh et al. (2001), protozoan faecal pellets did not contribute to carbon export. Thus, retention and regeneration of nutrients resulted from both protozoan grazing and from the heterotrophic utilization of their faecal pellets.

Small copepod pellets also did not contribute to carbon export during the early summer bloom. This is consistent with the emerging consensus that copepods retard flux due to their diverse feeding mechanisms such as coprophagy, sloppy feeding, and the production of slow-sinking faecal pellets (Peinert et al. 1982, Smetacek et al. 1990, Le Fèvre et al. 1998, Dubischar et al. 2002). In contrast, Bienfang and Ziemann (1992) concluded that much of the production in coastal high latitude waters is exported to depth due to the predominance of microphytoplankton blooms and grazing by mesozooplankton. This difference suggests that the influence of small copepods on carbon flux is more similar to protozoa than mesozooplankton. Like Smetacek et al. (1990), my results indicate that small copepods play a crucial role in the microbial network and the regeneration of nutrients. This was most marked later in the season when, despite their low biomass, copepod faecal pellet carbon was relatively high compared to that of protozoan pellets and sedimenting phytoplankton in the upper 10 m of the water column. Oval pellets produced by *Oithona similis* and harpacticoids (see Chapter 4) comprised most of the faecal pellet carbon, and these copepods were abundant in upper waters at this time. It has been reported

that *Oithona similis* preferentially grazes motile prey, clearing ciliates and flagellates at higher rates than diatoms (Atkinson 1995, 1996). These food sources were abundant during the latter half of summer, probably leading to high production of faecal pellets due to the low GGE of this small copepod. In addition, harpacticoids and *O. similis* have been found in sea-ice (Bergmans et al. 1991, Swadling 1998, Schnack-Schiel et al. 2001). Therefore, some of the pellets observed in the water column could have been released into the water column during ice-melt, or also transported into the study site with an input of freshwater that occurred at this time (see Chapter 3).

It has been generally accepted that faecal pellets produced by grazers contribute substantially to carbon flux (e.g. Honjo & Roman 1978, Turner & Ferrante 1979, Urrère & Knauer 1981, Longhurst & Harrison 1989). However, recent recognition that much of the faecal material produced in the oceans contributes to the retention of carbon in upper waters has led to a paradigm shift. Direct sedimentation of large phytoplankton cells and aggregates are now recognised as responsible for most of the carbon exported to depth (Legendre & Rassoulzadegan 1996, Smetacek 2000, Turner 2002).

Ice-algae are a considerable source of large phytoplankton and aggregates. During ice-melt and the decline of ice algal blooms, phytoplankton cells and aggregates are released and sink rapidly (Smetacek 1985, von Bodungen et al. 1986, Asper & Smith 1999). In Ellis Fjord, I also observed that the sedimentation of large ice-algae at the beginning of summer was responsible for the only notable carbon export throughout the season and represented almost 70% of the total POC flux (see Chapter 5). Release of ice-algae to the water column was sporadic and brief, occurring at the beginning of summer when protozoan biomass was relatively low. These aggregates most likely sedimented rapidly to depth and escaped grazing by microzooplankton.

Protozoan biomass increased during the phytoplankton bloom and exceeded that of phytoplankton by late summer when the bloom declined. Aggregates probably also formed during the decline of the phytoplankton bloom in late summer (see Chapter 5). However, the resulting carbon export was negligible as the lowest flux of POC to the lower water column was measured at this time. Stratification of the water column could have contributed to the retention of particles in upper waters. In addition,

protozoa reportedly feed on aggregates, converting them into smaller particles with reduced sinking speeds (Asper & Smith 1999). Heterotrophic flagellates were also abundant at this time (see Chapter 5) and *Oithona similis*, which feeds on flagellates, faecal pellets and detritus (Drits & Semenova 1994, González & Smetacek 1994, Asper & Smith 1999) was highly abundant in upper waters during the latter part of the season. Despite the high flux rates of carbon in upper waters during late summer, model calculations and microscope analyses showed that >90% of this POC was composed of detritus. This suggests recycling of matter occurred, with much of the sedimenting bloom being remineralised by nano- and microzooplankon in the water column.

6.5 Concluding remarks

The only notable export of carbon observed in Ellis Fjord resulted from summer warming that led to the release of large ice-algal cells and aggregates that sedimented rapidly through the water column. Most of the phytoplankton carbon was retained as a result of respiration, and the production of faecal pellets, by the dominant grazers. It is increasingly recognised that the physical environment is important in determining community composition and structure, and, therefore, export or retention (Bloesch & Burgi 1989, Legendre & Le Fèvre 1989, Kang & Lee 1995, Moline & Prézelin 1996, Verity & Smetacek 1996). Furthermore, it has been suggested that physical mixing and physico-chemical aggregation processes primarily determine carbon flux and there is little or no food web control (Rivkin et al. 1996, Tian et al. 2001). My study also showed that the change in food web structure over the season did not influence flux. However, the dominance of microzooplankton (protozoa and copepods) in Ellis Fjord resulted in the retention of carbon in the water column rather than carbon export. This contrasts with krill dominated communities in the Southern Ocean that contribute to substantial sedimentation of carbon via their faecal pellets and moults (von Bodungen et al. 1987, Lutter et al. 1989, Nicol & Stolp 1989, Riebesell et al. 1995). Therefore, the overall trophic structure of the community may not determine carbon flux *per se*. Instead, it is the species composition of auto- and heterotrophs that comprise the community that are instrumental in determining the export or retention of biogenic carbon in pelagic waters (Verity & Smetacek 1996, Wassmann 1998).

In Ellis Fjord, carbon export is episodic and most of the biogenic carbon is channelled into respiration and secondary production. This agrees with the general scenario of a regenerating system that has been described for the Southern Ocean (Smetacek et al. 1990). Similar to the findings of Smetacek et al. (1990), regeneration in Ellis Fjord was independent of episodic blooms. Regeneration predominated even during microphytoplankton blooms, due to the dominance of the grazer community by microzooplankton. Therefore, copepods and protozoa maintain a relatively steady-state system in which nutrients are recycled in upper waters (Smetacek et al. 1990, Paffenhöfer 1993, Williams et al. 1994, Nielsen & Sabatini 1996). My study shows that this can occur when nanoplankton and microbial trophic networks dominate, but also when microphytoplankton and herbivory prevail. This indicates that, in contrast to the general view (see above), food webs based on large phytoplankton do not always contribute to export production, but, like microbially based food webs, they can contribute to highly regenerative systems.

Conclusions

Global warming due to anthropogenic release of greenhouse gases has led to a surge of scientific interest in the mechanisms that mediate the concentration of CO_2 in the atmosphere. With an annual uptake of atmospheric CO_2 estimated to be around 2 Gt C yr^{-1} (Siegenthaler & Sarmiento 1993), the world's oceans are principal sinks for atmospheric CO_2. Models indicate that most of the draw-down of atmospheric CO_2 occurs in the Southern Ocean (Sarmiento & Le Quéré 1996). The marine biota play a pivotal role in the export of carbon from surface waters to the deep ocean, where it is sequestered for long time periods (Denman et al. 1996, Marchant et al. 2001). However, the biological processes that facilitate and moderate CO_2 draw-down are poorly understood. This thesis examines the role of planktonic interactions in Antarctic waters, and how community structure and function regulate vertical carbon flux.

The study was conducted in Ellis Fjord, a semi-isolated marine inlet that supports a zooplankton community of low species richness dominated by microzooplankton. As such, it provided a 'pseudo-macrocosm' in which the role of microzooplankton and protistan interactions in vertical carbon flux could be examined at fine spatial and temporal scales over an Antarctic summer. The seasonal succession of the plankton community in Ellis Fjord was similar to that commonly observed in the wider Southern Ocean. Over summer it changed from a classical Antarctic food web that was dominated by microplanktonic diatoms and small herbivorous copepods, to a microbially dominated food web comprising mainly nanoflagellates and protozoa. However, the community composition in Ellis Fjord differed from that in the open ocean. In Southern Ocean waters, microplankton blooms are commonly superimposed upon a background of nanoplankton (Smetacek et al. 1990, Bathmann et al. 1997, Waters et al. 2000). In contrast, blooms of nanoplankton in Ellis Fjord were superimposed upon a background of microplankton, probably due to the dominance of protozoa and small copepods that can graze nanoplankton more efficiently than they can graze microplankton. In addition, the biomass of protozoa was high and that of

small copepods was low compared to that generally reported in Antarctic waters.

While little is known about the complex interactions between protozoa and copepods, they graze similar food and therefore are likely to be trophic competitors, and they are also mutual predators (Sanders & Wickham 1993, Jeong 1994, Atkinson 1995, Lonsdale et al. 2000). Protozoan biomass is reportedly highest when melting ice stabilizes the water column, while more turbulent waters may favour the development of high copepod biomass (Nöthig 1988, Dubischar et al. 2002, Chapter 6). To my knowledge, this thesis provides the first examination in taxonomic detail of the relationship between the *in situ* biomass of both protozoa and small copepods over time. My study indicates that, together, the trophic interactions and physical environment may result in an inverse relationship between the biomass of protozoa and small copepods. Similarly, other reports of protozoan and small copepod biomass obtained simultaneously in space and time also show a negative relationship (Nöthig 1988, Archer et al. 1996a, Schnack-Schiel et al. 1998b, Swadling 1998). While the gross growth efficiencies (GGEs) of small copepods are lower than those of protozoa, the grazing impact of protozoa tends to exceed that of small copepods due to the capacity of protozoa to develop higher standing stocks. Therefore, increased ice-melt due to global warming could increase the biomass of protozoa relative to that of small copepods, resulting in the substantial depletion of phytoplankton and a reduction in carbon draw-down in polar waters. Further research is required to determine the interactions between protozoa, small copepods, and the physical environment.

The role of the physical environment in determining planktonic community composition was also reflected at the species level. *Oithona similis* and *Oncaea curvata* dominate small copepod biomass in the Southern Ocean, and due to their size and abundance, they are often considered as a single functional group. While aspects of their ecology are similar, such as the presence of mixed cohorts and overlapping generations year-round, their distributions appear distinct. In general, *O. similis* dominates in the open ocean, while *O. curvata* is dominant in near-shore coastal waters (e.g. Swadling et al. 1997, Atkinson 1998, Schnack-Schiel et al. 1998b, Dubischar et al. 2002, Chapter 3).

The relative dominance of either species is perhaps driven by differences in their behavioural ecology. *Oithona similis* has a much lower swimming velocity than *Oncaea* spp. (Drits & Semenova 1984, Paffenhöfer 1993), and may rely on turbulent mixing in the upper water column to maintain the population in waters where food is abundant. This is supported by the observation that, in Antarctic waters, *O. similis* is reportedly epipelagic, feeding on ice-associated production and resuspended particles in the upper water column (e.g. Hopkins 1985a, Hoshiai et al. 1991, González et al. 1994a, Atkinson 1995, Atkinson et al. 1996, Metz 1996, Atkinson & Sinclair 2000). In contrast, *O. curvata* appears more motile and can feed on episodic food sources such as aggregates (Ohtsuka & Kubo 1991, Paffenhöfer 1993, Metz 1996, Beaumont unpubl data). This species generally occupies deeper waters and appears able to develop substantial biomass in a relatively stable water column.

The low GGEs of these species suggest that, in high abundance such as that commonly observed in the Southern Ocean, their grazing impact on primary production could be substantial (Dubischar et al. 2002, Chapter 6). However, such high grazing pressure has not been observed *in situ* (Swadling et al. 1997, Razouls et al. 1998). Much remains to be understood regarding the ecology of *O. similis* and *O. curvata*, including the extent of omnivory by these species. Further, detailed studies of their ecology and interactions with higher trophic levels may assist in explaining this paradox of high biomass but low grazing pressure.

This thesis contains one of the first detailed investigations of microzooplankton faecal pellets. Substantial inter-specific and inter-taxa differences in faecal pellet morphology, ultrastructure, and carbon content were observed. Surprisingly, protozoan pellets that contained only empty diatom frustules contained more carbon per pellet than small oval copepod pellets. Importantly, the magnitude of protozoan pellet carbon was $1/50^{th}$ of that estimated in previous studies, indicating that the contribution by protozoan pellets to carbon flux in Antarctic waters has been greatly over-estimated. Minipellets were the only pellets observed at depth in the water column. However, many of these appeared to be 'false' minipellets caused by coprophagy and degradation, and contained little carbon. Therefore, both protozoan and small copepod faecal pellets, due to their structure and

morphology, did not contribute to vertical carbon flux but were remineralised in the water column.

Large diatom cells (ice-algae) and aggregates were the only substantial contributors to the flux of carbon to depth in Ellis Fjord. However, other protists did sediment. In particular, heterotrophic nanoflagellates contributed substantially to the numerical abundance of protists collected in sediment traps. This contrasts with the general view that only large, heavily silicified cells sink, and small cells remain suspended in the upper water column (Smayda 1970, Ittekot 1996, Smetacek 2000). While the sedimentation of heterotrophic nanoflagellates did not contribute significantly to vertical carbon flux, it may play a role in facilitating the regeneration of material in deeper waters, thereby contributing to reduced carbon export. In Ellis Fjord, sedimentation of microplanktonic diatoms was rapid but a lag was observed between the diatom bloom and sedimentation. Sedimentation of protists from the water column was affected by cell size, physiology, and predation. As a result, the composition of phytoplankton collected by sediment traps at a single point in time did not reflect the community composition of the overlying water column. This emphasises the importance of sampling the overlying water column during trap deployment, and the need for fine-scale spatial and temporal sampling to elucidate the processes that regulate the magnitude of vertical carbon flux.

Despite a change in food web structure over summer, most of the phytoplankton carbon in Ellis Fjord was retained in the upper water column as a result of respiration and the production of faecal pellets by microzooplankton grazers. This finding agrees with recent reports that there is little or no food web control of biogenic carbon flux (Rivkin et al. 1996, Tian et al. 2001). Instead, it is the relative composition of auto- and heterotrophs that comprise the community that determine the relative magnitude of carbon export or retention in pelagic waters (Verity & Smetacek 1996, Wassmann 1998). It has generally been accepted that communities dominated by microzooplankton, in association with microbial food webs, contribute to the regeneration of production (e.g. Smetacek et al. 1990). However, I found that this could also occur when microphytoplankton and herbivorous trophic networks prevail.

This study has shown that the composition, structure and function of plankton communities are instrumental in regulating the magnitude of carbon export in the Southern Ocean. Microbes, nanoplankton and microzooplankton comprise most of the labile carbon in the Southern Ocean. However, their contribution to the export of carbon to deep waters appears minimal. Instead, large phytoplankton and mesozooplankton, that comprise substantially lower biomass, are responsible for most of the vertical carbon flux. Therefore, localized changes in the proportion of nanoplankton, protozoa, and small copepods relative to large diatoms, aggregates and mesozooplankton may substantially affect carbon draw-down in the Southern Ocean.

At a broader scale, it has been shown that increased UV irradiances, resulting from ozone depletion due to greenhouse gases, reduce the abundance of diatoms and enhance concentrations of protozoa (Davidson & Belbin 2002), and it appears that copepods are generally less susceptible to UV-induced physiological damage and mortality than larger taxa such as Antarctic krill (*Euphausia superba*) (Jarman et al. 1999, Newman et al. 1999, Leech & Williamson 2000, Rautio & Korhola 2002). Furthermore, long-term predictions indicate that changes due to global warming will lead to an overall reduction in the net biological production in the Southern Ocean, with detrimental effects to higher trophic levels (Marchant et al. 2001). My results suggest that changes in planktonic community structure and function in the Southern Ocean that are induced by global warming and ozone depletion are likely to result in the exacerbation, rather than mitigation, of global climate change.

References

Adamson DA, Pickard J (1986a) Physiography and geomorphology of the Vestfold Hills. In JE Pickard (ed) Antarctic oasis: Terrestrial environments and history of the Vestfold Hills. Academic Press, Sydney, p 99-139

Adamson DA, Pickard J (1986b) Cainozoic history of the Vestfold Hills. In JE Pickard (ed) Antarctic oasis: Terrestrial environments and history of the Vestfold Hills. Academic Press, Sydney, p 63-67

Adrian R (1987) Viability of phytoplankton in fecal pellets of two cyclopoid copepods. Archiv für hydrobiologie 110: 321-330

Aksnes DL, Wassmann P (1993) Modeling the significance of zooplankton grazing for export production. Limnology and Oceanography 38: 978-985

Alder VA, Boltovskoy D (1993) The ecology of larger microzooplankton in the Weddell-Scotia Confluence area: horizontal and vertical distribution patterns. Journal of Marine Research 51: 323-344

Anadón R, Alvarez-Marques F, Fernandez E, Varela M, Zapata M, Gasol JM, Vaque D (2002) Vertical biogenic particle flux during Austral summer in the Antarctic Peninsula area. Deep-Sea Research 49: 883-901

Andreassen I, Nöthig E-M, Wassmann P (1996) Vertical particle flux on the shelf off northern Spitsbergen, Norway. Marine Ecology Progress Series 137: 215-228

Andreassen IJ, Wassmann P, Ratkova TN (1999) Seasonal variation of vertical flux of phytoplankton and biogenic matter at Nordvestbanken, north Norwegian shelf in 1994. Sarsia 84: 227-238

Archer SD, Leakey RJG, Burkill PH, Sleigh MA (1996a) Microbial dynamics in coastal waters of East Antarctica: herbivory by heterotrophic dinoflagellates. Marine Ecology Progress Series 130: 239-255

Archer SD, Leakey RJ, Burkill PH, Sleigh MA, Appleby CJ (1996b) Microbial ecology of sea ice at a coastal Antarctic site: community composition, biomass and temporal change. Marine Ecology Progress Series 135: 179-195

Arrigo KR, Robinson DH, Worthen DL, Dunbar RB, DiTullio GR, VanWoert M, Lizotte MP (1999) Phytoplankton community structure and the drawdown of nutrients and CO_2 in the Southern Ocean. Science 283: 365-367

Asper VL, Smith Jr. WO (1999) Particle fluxes during austral spring and summer in the southern Ross Sea, Antarctica. Journal of Geophysical Research 104: 5345-5359

Atkinson A (1995) Omnivory and feeding selectivity in five copepod species during spring in the Bellinghausen Sea, Antarctica. ICES Journal of Marine Science 52: 385-396

Atkinson A (1996) Subantarctic copepods in an oceanic, low chlorophyll environment: ciliate predation, food selectivity and impact on prey populations. Marine Ecology Progress Series 130: 85-96

Atkinson A (1998) Life cycle strategies of epipelagic copepods in the Southern Ocean. Journal of Marine Systems 15: 289-311

Atkinson A, Shreeve RS, Pakhomov EA, Priddle J, Blight SP, Ward P (1996) Zooplankton response to a phytoplankton bloom near South Georgia, Antarctica. Mar Ecol Prog Ser 144: 195-210

Atkinson A, Schnack-Schiel SB, Ward P, Marin V (1997) Regional differences in the life cycle of *Calanoides acutus* (Copepoda: Calanoida) within the Atlantic sector of the Southern Ocean. Marine Ecology Progress Series 150: 99-111

Atkinson A, Shreeve RS (1995) Response of the copepod community to a spring bloom in the Bellinghausen Sea. Deep-Sea Research II 42: 1291-1311

Atkinson A, Sinclair JD (2000) Zonal distribution and seasonal vertical migration of copepod assemblages in the Scotia Sea. Polar Biology 23: 46-58

Azam F (1998) Microbial control of oceanic carbon flux: the plot thickens. Science 280: 694-696

Båmstedt U (1986) Chemical composition and energy content. In EDS Corner, SCM O'Hara (eds) The biological chemistry of marine copepods. Clarendon Press, Oxford, p 1-58

Banse K (1990) New views on the degradation and disposition of organic particles as collected by sediment traps in the open sea. Deep-Sea Research 37: 1177-1195

Banse K (1992) Grazing, temporal changes of phytoplankton concentrations, and the microbial loop in the open sea. In PG Falkowski, AD Woodhead (eds) Primary productivity and biogeochemical cycles in the sea. Plenum Press, New York, p 409-440

Banse K (1994) Grazing and zooplankton production as key controls of phytoplankton production in the open ocean. Oceanography 7: 13-20

Banse K (1995a) Zooplankton: pivotal role in the control of ocean production. ICES Journal of Marine Science 52: 265-277

Banse K (1995b) Antarctic marine top predators revisited: homeotherms do not leak much CO_2 to the air. Polar Biology 15: 93-104

Barnes RD (1987) Invertebrate zoology. CBS College Publishing, Philadelphia, 893 pp

Bathmann U, Fischer G, Müller PJ, Gerdes D (1991) Short-term variations in particulate matter sedimentation off Kapp Norvegia, Weddell Sea, Antarctica: relation to water mass advection, ice cover, plankton biomass and feeding activity. Polar Biology 11: 185-195

Bathmann U, Liebezeit G (1986) Chlorophyll in copepod faecal pellets: changes in pellet numbers and pigment content during a declining Baltic spring bloom. P.S.Z.N.I. Marine Ecology 7: 59-73

Bathmann UV (1996) Abiotic and biotic forcing on vertical particle flux in the Southern Ocean. In P S V Ittekot, S Honjo, PJ Depetris (eds), Particle flux in the ocean. John Wiley and Sons Ltd., Chichester, p 243-250

Bathmann UV, Noji TT, Voss M, Peinert R (1987) Copepod fecal pellets: abundance, sedimentation and content at a permanent station in the Norwegian Sea in May/June 1986. Marine Ecology Progress Series 38: 45-51

Bathmann UV, Scharek R, Klaas C, Dubischar CD, Smetacek V (1997) Spring development of phytoplankton biomass and composition in major water masses of the Atlantic sector of the Southern Ocean. Deep-Sea Research 44: 51-67

Battarbee RW (1986) Diatom analysis. In BE Berglund (ed) Handbook of Holocene Palaeoecology and Palaeohydrology. John Wiley & Sons Ltd., Chichester, p 527-570

Bayly IAE (1986) Ecology of the zooplankton of a meromictic antarctic lagoon with special reference to *Drepanopus bispinosus* (Copepoda: Calanoida). Hydrobiologia 140: 199-231

Beaumont KL, Hosie GW (1997) Mesoscale distribution and abundance of four pelagic copepod species in Prydz Bay. Antarctic Science 9: 121-133

Beaumont KL, Plummer AJ, Hosie GW, Ritz DA (2001) Production and fate of faecal pellets during summer in an East Antarctic fjord. Hydrobiologia 453/454: 55-65

Becquevort S, Mathot S, Lancelot C (1992) Interactions in the microbial community of the marginal ice zone of the northwestern Weddell Sea through size distribution analysis. Polar Biology 12: 211-218

Becquevort S, Menon P, Lancelot C (2000) Differences of the protozoan biomass and grazing during spring and summer in the Indian sector of the Southern Ocean. Polar Biology 23: 309-320

Becquevort S, Smith Jr. WO (2001) Aggregation, sedimentation and biodegradability of phytoplankton-derived material during spring in the Ross Sea, Antarctica. Deep-Sea Research 48: 4155-4178

Bergmans M, Dahms HU, Schminke HK (1991) An *r*-strategist in Antarctic pack ice. Oecologia 86: 305-309

Bianchi A, Garcin J, Gorsky G, Poulicek M, Tholosan O (1999) Stimulation of the potential heterotrophic activity in deep seawater by barotolerant bacteria colonizing faecal pellets produced by migrating zooplankton. C.R. Acad. Sci. Paris, Sciences de la vie / Life Sciences 322: 1113-1120

Bienfang PK (1980) Herbivore diet affects fecal pellet settling. Canadian Journal of Fisheries and Aquatic Sciences 37: 1352-1357

Bienfang PK, Ziemann DA (1992) The role of coastal high latitude ecosystems in global export production. In PG Falkowski, AD Woodhead (eds) Primary productivity and biogeochemical cycles in the sea. Plenum Press, New York, p 285-297

Billen G, Becquevort S. (1991). *Phytoplankton-bacteria relationship in the Antarctic marine ecosystem.* Paper presented at the Proceedings of the Pro Mare Symposium on Polar Marine Ecology, Trondheim, 12-16 May 1990.

Billett DSM, Lampitt RS, Rice AL, Mantoura RFC (1983) Seasonal sedimentation of phytoplankton to the deep-sea benthos. Nature 302: 520-522

Bjørnsen PK, Kuparinen J (1991) Growth and herbivory by heterotrophic dinoflagellates in the Southern Ocean, studied by microcosm experiments. Marine Biology 109: 397-405

Bloesch J (1988). Sediment trap design and vertical flux studies. Paper presented at the Sediment trap studies in the Nordic countries, Tvarminne Zoological Station, Hanko, Finland

Bloesch J (1995) Mechanisms, measurement and importance of sediment resuspension in lakes. Marine and Freshwater Research 46: 295-304

Bloesch J (1996) Towards a new generation of sediment traps and a better measurement/understanding of settling particle flux in lakes and oceans: a hydrodynamical protocol. Aquatic Sciences 58: 283-296

Bloesch J, Burgi H-R (1989) Changes in phytoplankton and zooplankton biomass and composition reflected by sedimentation. Limnology and Oceanography 34: 1048-1061

Bloesch J, Burns NM (1980) A critical review of sedimentation trap technique. Schweizerische Zeitschnft fuer Hydrologie 42: 15-55

Boden BP (1985) The South African SIBEX I Cruise to the Prydz Bay region, 1984: VIII. The plankton encountered during the survey. South African Journal of Antarctic Research 15: 28-32

Boero F (1994) Fluctuations and variations in coastal marine environments. P.S.Z.N.I. Marine Ecology 15: 3-25

Bosch I, Beauchamp KA, Steele ME, Pearse JS (1987) Development, metamorphosis, and seasonal abundance of embryos and larvae of the Antarctic sea urchin *Sterechinus neumayerii*. Biological Bulletin 173: 126-135

Böttger R, Schnack D (1986) On the effect of formaldehyde fixation on the dry weight of copepods. Meeresforschung 31: 141-152

Bowman JP, Brown MV, Nichols PD (1997a) Biodiversity and ecophysiology of bacteria associated with Antarctic sea ice. Antarctic Science 9: 134-142

Bowman JP, McCammon SA, Brown MV, Nichols DS, McMeekin TA (1997b) Diversity and association of psychrophilic bacteria in Antarctic sea ice. Applied and Environmental Microbiology 63: 3068-3078

Bray JR, Curtis JT (1957) An ordination of the upland forest communities of southern Wisconsin. Ecological Monographs 27: 325-349

Brey T (1991) Population dynamics of *Sterechinus antarcticus* (Echinodermata: Echinoida) on the Weddell Sea shelf and slope, Antarctica. Antarctic Science 251: 251-256

Brey T, Gutt J (1991) The genus *Sterechinus* (Echinodermata: Echinoida) on the Weddell Sea shelf and slope (Antarctica): distribution, abundance and biomass. Polar Biology 11: 227-232

Brock TD (1978) The poisoned control in biogeochemical investigations. In WE Krumbein (ed) Environmental biogeochemistry and geomicrobiology. Ann Arbor Science Publishers Inc., Ann Arbor, p 717-725

Brockington S, Clarke A (2001) The relative influence of temperature and food on the metabolism of a marine invertebrate. Journal of Experimental and Marine Biology 258: 87-99

Brown TJ, Sibert JR (1977) Food of some benthic harpacticoid copepods. Journal of the Fisheries Research Board Canada 34: 1028-1031

Brush MJ, Brawley JW, Nixon SW, & Kremer JN (2002) Modeling phytoplankton production: problems with the Eppley curve and an empirical alternative. Marine Ecology Progress Series 238: 31-45

Buck KR, Bolt PA, Garrison DL (1990) Phagotrophy and fecal pellet production by an athecate dinoflagellate in Antarctic sea ice. Marine Ecology Progress Series 60: 75-84

Buck KR, Newton J (1995) Fecal pellet flux in Dabob Bay during a diatom bloom: contribution of microzooplankton. Limnology and Oceanography 40: 306-315

Buesseler KO (1991) Do upper-ocean sediment traps provide an accurate record of particle flux? Nature 353: 420-423

Buma AGJ, Gieskes WWC, Thomsen HA (1992) Abundance of Cryptophyceae and chlorophyll *b*-containing organisms in the Weddell-Scotia Confluence area in the spring of 1988. Polar Biology 12: 43-52

Burke CM, Burton HR (1988) Photosynthetic bacteria in meromictic lakes and stratified fjords of the Vestfold Hills, Antarctica. In JM Ferris, HR Burton, GW Johnstone, IAE Bayly (eds) Biology of the Vestfold Hills, Antarctica. Kluwer Academic Publishers, London, p 13-23

Burkill PH, Edwards ES, Sleigh MA (1995) Microzooplankton and their role in controlling phytoplankton growth in the marginal ice zone of the Bellingshausen Sea. Deep-Sea Research II 42: 1277-1290

Cadée GC (1992) Organic carbon in the upper layer and its sedimentation during the ice retreat period in the Scotia-Weddell Sea, 1988. Polar Biology 12: 253-259

Cadée GC, González H, Schnack-Schiel SB (1992) Krill diet affects faecal string settling. Polar Biology 12: 75-80

Cailliau C, Belviso S, Goutx M, Bedo A, Park Y, Charriaud E (1999) Sedimentation pathways in the Indian sector of the Southern Ocean during a production regime dominated by regeneration. Marine Ecology Progress Series 190: 53-67

Caron D (1991) Heterotrophic flagellates associated with sedimenting detritus. In DJ Patterson, J Larsen (eds) The biology of free-living heterotrophic flagellates. Clarendon Press, Oxford, p 77-92

Caron DA, Goldman JC, Dennett MR (1990) Carbon utilization by the omnivorous flagellate *Paraphysomonas imperforata*. Limnology and Oceanography 35: 192-201

Carrada GC, Mangoni O, Russo GF, Saggiomo V (2000) Phytoplankton size-fractionated biomass in the Ross Sea: spatial and temporal variations during the austral spring. In Faranda, Guglielmo, Ianora (eds) Ross Sea Ecology. Springer-Verlag, Berlin Heidelberg, p 205-216

Carroll ML, Miquel J-C, Fowler SW (1998) Seasonal patterns and depth-specific trends of zooplankton fecal pellet fluxes in the Northwestern Mediterranean Sea. Deep-Sea Research I 45: 1303-1318

Christian JR, Karl DM (1995) Measuring bacterial ectoenzyme activities in marine waters using mercuric chloride as a preservative and a control. Marine Ecology Progress Series 123: 217-224

Coale KH (1990) Labyrinth of doom: a device to minimize the "swimmer" component in sediment trap collections. Limnology and Oceanography 35: 1376-1381

Cripps GC, Clarke A (1998) Seasonal variation in the biochemical composition of particulate material collected by sediment traps at Signy Island, Antarctica. Polar Biology 20: 414-423

Dahms H (1993) Internal anatomy of female *Paramphiascella fulvofasciata* (Copepoda, Harpacticoida). Canadian Journal of Zoology 71: 1242-1250

Dahms H, Bergmans M, Schminke HK (1990) Distribution and adaptations of sea ice inhabiting Harpacticoida (Crustacea, Copepoda) of the Weddell Sea (Antarctica). P.S.Z.N.I: Marine Ecology 11: 207-226

Davidson AT, Belbin L (2002) Exposure of natural Antarctic marine microbial assemblages to ambient UV radiation: effects on the marine microbial community. Aquatic Microbial Ecology 27: 159-174

Davidson AT, Marchant HJ (1992) Protist abundance and carbon concentration during a *Phaeocystis*-dominated bloom at an Antarctic coastal site. Polar Biology 12: 387-395

Delille D, Fiala M, Kuparinen J, Kuosa H, Plessis C (2002) Seasonal changes in microbial biomass in the first-year ice of the Terre Adelie area (Antarctica). Aquatic Microbial Ecology 28: 257-265

Delille D, Fiala M, Rosiers C (1995) Seasonal changes in phytoplankton and bacterioplankton distribution at the ice-water interface in the Antarctic neritic area. Marine Ecology Progress Series 123: 225-233

Denman K, Hofmann E, Marchant HJ (1996) Marine biotic response to environmental change and feedbacks to climate. In JT Houghton, LG Meira Filho, BA Callander, N Harris, A Kattenberg, K Maskill (eds) Climate change 1995 The Science of Climate Change. IPCC, Cambridge University Press, p 483-516

Drits AV, Semenova TN (1984) Experimental investigations of the feeding of *Oithona similis* Claus. Oceanology (English version) 24: 755-759

Dubischar CD, Bathmann UV (1997) Grazing impact of copepods and salps on phytoplankton in the Atlantic sector of the Southern Ocean. Deep-Sea Research 44: 415-433

Dubischar CD, Lopes RM, Bathmann UV (2002) High summer abundances of small pelagic copepods at the Antarctic Polar Front - implications for ecosystem dynamics. Deep-Sea Research 49: 3871-3887

Dunbar RB, Leventer A, Stockton W (1989) Biogenic sedimentation in McMurdo Sound, Antarctica. Marine Geology 85: 155-179

Elbrächter M (1988) Life cycle of *Schizochytriodinium calani* nov. gen. nov. spec., a dinoflagellate parasitizing copepod eggs. Helgolander Meeresunters 42: 593-599

Elbrächter M (1991) Faeces production by dinoflagellates and other small flagellates. Marine Microbial Food Webs 5: 189-204

Eslake D, Kirkwood R, Burton H, Zipan W (1991) Temporal changes in zooplankton composition in a hypersaline Antarctic lake subject to periodic seawater incursions. Hydrobiologia 210: 93-99

Fabiano M, Chiantore M, Povero P, Cattaneo-Vietti R, Pusceddu A, Misic C, Albertelli G (1997) Short-term variations in particulate matter flux in Terra Nova Bay, Ross Sea. Antarctic Science 9: 143-149

Falkowski PG, Barber RT, Smetacek V (1998) Biogeochemical controls and feedbacks on ocean primary production. Science 281: 200 - 206

Falkowski P, Scholes RJ, Boyle E, Canadell J, Canfield D, Elser J, Gruber N, Hibbard K, Hogberg P, Linder S, Mackenzie FT, Moore III B, Pedersen T, Rosenthal Y, Seitzinger S, Smetacek V, Steffen W (2000) The global carbon cycle: a test of our knowledge of earth as a system. Science 290: 291-296

Feinberg LR, Dam HG (1998) Effects of diet on dimensions, density and sinking rates of fecal pellets of the copepod *Acartia tonsa*. Marine Ecology Progress Series 175: 87-96

Fenchel T (1988) Marine plankton food chains. Annual Review Ecological Systems 19: 19-38

Fiala M, Semeneh M, Oriol L (1998) Size-fractionated phytoplankton biomass and species composition in the Indian sector of the Southern Ocean during austral summer. Journal of Marine Systems 17: 179-194

Field JG, Clarke KR, Warwick RM (1982) A practical strategy for analysing multispecies distribution patterns. Marine Ecology Progress Series 8: 37-52

Fortier L, Le Fèvre J, Legendre L (1994) Export of biogenic carbon to fish and to the deep ocean: the role of large planktonic microphages. Journal of Plankton Research 16: 809-839

Fowler SW, Knauer GA (1986) Role of large particles in the transport of elements and organic compounds through the oceanic water column. Progress in Oceanography 16: 147-194

Fransz HG (1988) Vernal abundance, structure and development of epipelagic copepod populations of the eastern Weddell Sea (Antarctica). Polar Biology 9: 107-114

Fransz HG, González SR (1995) The production of *Oithona similis* (Copepoda: Cylopoida) in the Southern Ocean. ICES Journal of Marine Science 52: 549-555

Froneman PW, Pakhomov EA, Perissinotto R, Laubscher RK, McQuaid CD (1997) Dynamics of the plankton communities of the Lazarev Sea (Southern Ocean) during seasonal ice melt. Marine Ecology Progress Series 149: 201-214

Froneman P, Perissinotto R (1996) Microzooplankton grazing in the Southern Ocean: implications for the carbon cycle. P.S.Z.N.I. Marine Ecology 17: 99-115

Fukuchi M, Tanimura A (1981) A preliminary note on the occurrence of copepods under sea ice near Syowa Station, Antarctica. Memoirs of the National Institue of Polar Research 34: 37-43

Gaines G, Taylor FJR (1984) Extracellular digestion in marine dinoflagellates. Journal of Plankton Research 6: 1057-1061

Gallagher JB, Burton H (1988) Seasonal mixing of Ellis Fjord, Vestfold Hills, East Antarctica. Estuarine, Coastal and Shelf Science 27: 363-380

Gallagher JB, Burton HR, Calf GE (1989) Meromixis in an antarctic fjord: a precursor to meromictic lakes on an isostatically rising coast. Hydrobiologia 172: 235-254

Gallienne CP, Robins DB (2001) Is *Oithona* the most important copepod in the world's oceans? Journal of Plankton Research 23: 1421-1432

Gardner WD, Hinga KR, Marra J (1983) Observations on the degradation of biogenic material in the deep ocean with implications on accuracy of sediment trap fluxes. Journal of Marine Research 41: 195-214

Gardner WD, Zhang Y (1997) The effect of brine on the collection efficiency of cylindrical sediment traps. Journal of Marine Research 55: 1029-1048

Garrison DL (1991) An overview of the abundance and role of protozooplankton in Antarctic waters. Journal of Marine Systems 2: 317-331

Garrison DL, Buck KR (1989) Protozooplankton in the Weddell Sea, Antarctica: abundance and distribution in the ice-edge zone. Polar Biology 9: 341-351

Garrison DL, Buck KR (1991) Surface-layer sea ice assemblages in Antarctic pack ice during the austral spring: environmental conditions, primary production and community structure. Marine Ecology Progress Series 75: 161-172

Garrison DL, Buck KR, Fryxell GA (1988) Algal assemblages in Antarctic pack ice and in ice-edge phytoplankton. Journal of Phycology 23: 564-572

Garrison DL, Gowing MM (1993) Protozooplankton. In E Imre Friedmann (ed) Antarctic microbiology. Wiley-Liss Inc., New York, p 123-165

Gerber RP, Gerber MB (1979) Ingestion of natural particulate organic matter and subsequent assimilation, respiration and growth by tropical lagoon zooplankton. Marine Biology 52: 33-43

Gibson JAE. (1998). Carbon flow through inshore marine environments of the Vestfold Hills, East Antarctica. ANARE Report 139, Australian Antarctic Division, Hobart, 224 pp

Gibson JAE (1999) The role of ice in determining mixing intensity in Ellis Fjord, Vestfold Hills, East Antarctica. Antarctic Science 11: 419-426

Gibson JAE, Swadling KM, Burton HR (1997) Interannual variation in dominant phytoplankton species and biomass near Davis station, East Antarctica. Proceedings of the NIPR Symposium on Polar Biology 10: 78-90

Gifford DJ (1991) The protozoan-metazoan link in pelagic ecosystems. Journal of Protozoology 38: 81-86

Godhe A, Noren F, Kuylenstierna M, Ekberg C, Karlson B (2001) Relationship between planktonic dinoflagellate abundance, cysts recovered in sediment traps and environmental factors in the Gullmar Fjord, Sweden. Journal of Plankton Research 23: 923-938

Goldman JC (1988) Spatial and temporal discontinuities of biological processes in pelagic surface waters. In B Rothschild (ed) Toward a theory on biological-physical interactions in the world ocean. Kluwer Academic Publishers, Dordrecht, p 273-296

González HE (1992a) The distribution and abundance of krill faecal material and oval pellets in the Scotia and Weddell Seas (Antarctica) and their role in particle flux. Polar Biology 12: 81-91

González HE (1992b) Distribution and abundance of minipellets around the Antarctic peninsula. Implications for protistan feeding behaviour. Marine Ecology Progress Series 90: 223-236

González HE, González SR, Brummer G-JA (1994b) Short-term sedimentation pattern of zooplankton, faeces and microplankton at a permanent station in the Bjornafjorden (Norway) during April-May 1992. Marine Ecology Progress Series 105: 31-45

González HE, Kurbjeweit F, Bathmann UV (1994a) Occurrence of cyclopoid copepods and faecal material in the Halley Bay region, Antarctica, during January-February 1991. Polar Biology 14: 331-342

González HE, Ortiz VC, Sobarzo M (2000) The role of faecal material in the particulate organic carbon flux in the northern Humboldt Current, Chile (23°S), before and during the 1997-1998 El Nino. Journal of Plankton Research 22: 499-529

González HE, Smetacek V (1994) The possible role of the cyclopoid copepod *Oithona* in retarding vertical flux of zooplankton faecal material. Marine Ecology Progress Series 113: 233-246

Gowing MM, Garrison DL, Kunze HB, Winchell CJ (2001) Biological components of Ross Sea short-term particle fluxes in the austral summer of 1995-1996. Deep-Sea Research I 48: 2645-2671

Gowing MM, Silver MW (1985) Minipellets: a new and abundant size class of marine fecal pellets. Journal of Marine Research 43: 395-418

Granéli E, Turner JT (2002) Top-down regulation in ctenophore-copepod-ciliate-diatom-phytoflagellate communities in coastal waters: a mesocosm study. Marine Ecology Progress Series 239: 57-68

Gray JS, Aschan M, Carr MR, Clarke KR, Green RH, Pearson TH, Rosenberg R, Warwick RM (1988) Analysis of community attributes of the benthic macrofauna of Frierfjord / Langesundfjord and in a mesocosm experiment. Marine Ecology Progress Series 46: 151-165

Grey J, Laybourn-Parry J, Leakey RJG, McMinn A (1997) Temporal patterns of protozooplankton abundance and their food in Ellis Fjord, Princess Elizabeth Land, Eastern Antarctica. Estuarine, Coastal and Shelf Science 45: 17-25

Guglielmo L, Carrada GC, Catalano G, Dell'Anno A, Fabiano M, Lazzara L, Mangoni O, Pusceddu A, Saggiomo V (2000) Structural and functional properties of sympagic communities in the annual sea ice at Terra Nova Bay (Ross Sea, Antarctica). Polar Biology 23: 137-146

Gunderson K. (1988). Degradation of organic matter in sediment traps. In P Wassmann, A-S Heiskanen (eds) Sediment trap studies in the Nordic countries 1, Tvarminne Zoological Station, Hanko, Finland, 24-28 February, 1988. p 22-37

Gunderson K. (1990). Sampling precision and preservation of sediment trap material. Paper presented at the Sediment traps in marine ecological reserach and monitoring, Kristineberg Marine Biological Station, Fiskebackskil, Sweden, p 6-35

Gunderson K, Lee C, Lundsgaard C, Passow U, Peinert R, Silver M, Thingstad TF (1990). Biological and chemical biases in sediment traps. Paper presented at the Sediment traps in marine ecological research and monitoring, Kristineberg Marine Biological Station, Fiskebackskil, Sweden, p 280-285

Gunderson K, Wassmann P (1990) Use of chlorofom in sediment traps: caution advised. Marine Ecology Progress Series 64: 187-195

Gunther S, George KH, Gleitz M (1999) High sympagic metazoan abundance in platelet layers at Drescher Inlet, Weddell Sea, Antarctica. Polar Biology 22: 82-89

Gust G, Byrne RH, Bernstein RE, Betzer PR, Bowles W (1992) Particle fluxes and moving fluids: experience from synchronous trap collections in the Saragasso Sea. Deep-Sea Research 39: 1071-1083

Gustafson Jr. DE, Stoecker DK, Johnson MD, Van Heukelem WF, Sneider K (2000) Cryptophyte algae are robbed of their organelles by the marine ciliate *Mesodinium rubrum*. Nature 405: 1049-1052

Hairston Jr. NG, Hairston Sr. NG (1993) Cause-effect relationships in energy flow, trophic structure, and interspecific interactions. The American Naturalist 142: 379-411

Hansen B, Fotel FL, Jensen NJ, Madsen SD (1996) Bacteria associated with a marine planktonic copepod in culture. II. Degradation of fecal pellets produced on a diatom, a nanoflagellate or a dinoflagellate diet. Journal of Plankton Research 18: 275-288

Hansen PJ (1992) Prey size selection, feeding rates and growth dynamics of heterotrophic dinoflagellates with special emphasis on *Gyrodinium spirale*. Marine Biology 114: 327-334

Hansen PJ, Calado AJ (1999) Phagotrophic mechanisms and prey selection in fee-living dinoflagellates. Journal of Eukaryotic Microbiology 46: 382-389

Harbison GR, Gilmer RW (1986) Effects of animal behaviour on sediment trap collections: implications for the calculation of aragonite fluxes. Deep-Sea Research 33: 1017-1024

Harbison GR, Madin LP, Swanberg NR (1978) On the natural history and distribution of oceanic ctenophores. Deep-Sea Res. 25: 233-256

Hargrave BT, von Bodungen B, Conover RJ, Fraser AJ, Phillips G, Vass WP (1989) Seasonal changes in sedimentation of particulate matter and lipid content of zooplankton collected by sediment trap in the Arctic Ocean off Axel Heiberg Island. Polar Biology 9: 467-475

Hayat MA (1989) Principles and techniques of electron microscopy. The Macmillan Press Ltd, London, 469 pp

Hedges JI, Lee C, Wakeham SG, Hernes PJ, Peterson ML (1993) Effects of poisons and preservatives on the fluxes and elemental compositions of sediment trap materials. Journal of Marine Research 51: 651-668

Heiskanen A-S, Haapala J, Gundersen K (1998) Sedimentation and pelagic retention of particulate C, N and P in the coastal northern Baltic Sea. Estuarine, Coastal and Shelf Science 46: 703-712

Hirst AG, Lampitt RS (1998) Towards a global model of *in situ* weight-specific growth in marine planktonic copepods. Marine Biology 132: 247-257

Hoegh-Guldberg O, Pearse JS (1995) Temperature, food availability, and the development of marine invertebrate larvae. American Zoologist 35: 415-425

Hofmann EE, Klinck JM, Paffenhöfer G-A (1981) Concentrations and vertical fluxes of zooplankton fecal pellets on a continental shelf. Marine Biology 61: 327-335

Holm-Hansen O, Mitchell BG (1991) Spatial and temporal distribution of phytoplankton and primary production in the western Bransfield Strait region. Deep-Sea Research 38: 961-980

Honjo S (1990) Particle fluxes and modern sedimentation in the polar oceans. In WO Smith Jr (ed) Polar Oceanography: Part B Chemistry, Biology and Geology. Academic Press, Inc., San Diego, p 687-739

Honjo S (1996) Fluxes of particles to the interior of the open oceans. In V Ittekkot, P Schafer, S Honjo, PJ Depetris (eds) Particle Flux in the Ocean. John Wiley and Sons Ltd, Chichester, p 91-154

Honjo S, Connell JF, Sachs PL (1980) Deep-ocean sediment trap; design and function of PARFLUX Mark II. Deep-Sea Research 27: 745-753

Honjo S, Roman MR (1978) Marine copepod fecal pellets: production, preservation and sedimentation. Journal of Marine Research 36: 45-57

Hopkins TL (1985) The zooplankton community of Croker Passage, Antarctic Peninsula. Polar Biology 4: 161-170

Hopkins TL (1987) Midwater food web in McMurdo Sound, Ross Sea, Antarctica. Marine Biology 96: 93-106

Hopkins TL, Ainley DG, Torres JJ, Lancraft TM (1993) Trophic structure in open waters of the marginal ice zone in the Scotia-Weddell confluence region during spring (1983). Polar Biology 13: 389-397

Hopkins TL, Torres JJ (1989) Midwater food web in the vicinity of a marginal ice zone in the western Weddell Sea. Deep-Sea Research 36: 543-560.

Horn H, Horn W (2000) Sedimentation - the main loss factor in waters dominated by diatoms. Results of long-term investigations. International Review of Hydrobiology 85: 191-208

Hoshiai T (1985) Autumnal proliferation of ice-algae in Antarctic sea-ice. In WR Siegfried, PR Condy, RM Laws (eds) Antarctic Nutrient Cycles and Food Webs. Springer-Verlag Berlin, Heidelberg,

Hoshiai T, Tanimura A (1981) Copepods in the stomach of a Nototheniid fish, *Trematomus borchgrevinki* Fry at Syowa Station, Antarctica. Memoirs of NIPR 34: 44-48

Hoshiai T, Tanimura A, Watanabe K (1987) Ice algae as food of an Antarctic ice-associated copepod, *Paralabidocera antarctica* (I.C. Thompson). Proceedings of the NIPR Symposium on Polar Biology 1: 105-111

Hoshiai T, Tanimura A, Watanabe K, Fukuchi M (1991) Algae-copepod-fish link associated with Antarctic sea ice. In J Mauchline, T Nemoto (eds) Marine Biology: its accomplishment and future prospect. p 237-246

Hosie GW (1994a). Multivariate analyses of the macrozooplankton community and euphausiid larval ecology in the Prydz Bay region, Antarctica. ANARE Report No 137, Antarctic Division, 209 pp

Hosie GW (1994b) The macrozooplankton communities in the Prydz Bay region, Antarctica. In SZ El-Sayed (ed) Southern Ocean Ecology: The BIOMASS Perspective. Cambridge University Press., Cambridge, p 93-123

Hosie GW, Cochran TG (1994) Mesoscale distribution patterns of macrozooplankton communtiies in Prydz Bay, Antarctica - January to February 1991. Marine Ecology Progress Series 106: 21-39

Hosie GW, Cochran TG, Pauly T, Beaumont KL, Wright SW, Kitchener JA (1997) Zooplankton community structure of Prydz Bay, Antarctica, January-February 1993. Proceedings of the NIPR Symposium on Polar Biology 10: 90-133.

Huntley ME, Lopez MDG (1992) Temperature-dependent production of marine copepods: a global synthesis. The American Naturalist 140: 201-242

Huntley ME, Lopez MDG, Karl DM (1991) Top predators in the Southern Ocean: a major leak in the biological carbon pump. Science 253: 64-66

Ikeda T, Kanno Y, Ozaki K, Shinada A (2001) Metabolic rates of epipelagic marine copepods as a function of body mass and temperature. Marine Biology 139: 587-596

Ishikawa A, Washiyama N, Tanimura A, Fukuchi M (2001) Variation in the diatom community under fast ice near Syowa Station, Antarctica, during the austral summer of 1997/98. Polar Bioscience 14: 10-23

Ittekot V (1996) Particle flux in the Ocean: Summary. In V Ittekot, P Schafer, S Honjo, PJ Depetris (eds) Particle flux in the ocean. John Wiley and Sons Ltd., Chichester, p 357-366

Jacobson DM, Anderson DM (1986) Thecate heterotrophic dinoflagellates: feeding behaviour and mechanisms. Journal of Phycology 22: 249-258

Jacques G, Panouse M (1991) Biomass and composition of size fractionated phytoplankton in the Weddell-Scotia confluence area. Polar Biology 11: 315-328

Jarman S, Elliott N, Nicol S, McMinn A, Newman S (1999) The base composition of the krill genome and its potential susceptibility to damage by UV-B. Antarctic Science 11: 23-26

Jeffrey SW, Humphrey GF (1975) New spectrophotometric equations for determining chlorophylls *a*, *b*, c_1 and c_2 in higher plants, algae and natural phytoplankton. Biochemie und Physiologie der Pflanzen 167: 191-194

Jeong HJ (1994) Predation by the heterotrophic dinoflagellate *Protoperidinium* cf. *divergens* on copepod eggs and early naupliar stages. Marine Ecology Progress Series 114: 203-208

Jongman RH, ter Braak CJF, van Tongren OFR (1987) Data analysis in community and landscape ecology. Pudoc Wageningen, Wageningen, 299 pp

Kang S-H, Lee SH (1995) Antarctic phytoplankton assemblage in the western Bransfield Strait region, February 1993: composition, biomass, and mesoscale distributions. Marine Ecology Progress Series 129: 253-267

Karl DM, Christian JR, Dore JE (1996) Microbiological oceanography in the region west of the Antarctic peninsula: microbial dynamics, nitrogen cycle and carbon flux. In Foundations for ecological research west of the Antarctic Peninsula. Antarctic Research Series 70: 303-332

Karl DM, Tilbrook BD, Tien G (1991) Seasonal coupling of organic matter production and particle flux in the western Bransfield Strait, Antarctica. Deep-Sea Research 38: 1097-1126

Kelley CA, Pakulski JD, Sandvik SLH, Coffin RB, Downer J, R.C., Aas P, Lyons MM, Jeffrey WH (1999) Phytoplanktonic and bacterial carbon pools and productivities in teh Grelache Strait, Antarctica, during early Austral Spring. Microbial Ecology 38: 296-305

Khripounoff A, Crassous P (1994) Particulate material degradation in sediment traps at 2000 m depth on the Meriadzeck Terrace (Bay of Biscay). Deep-Sea Research 41: 821-829

Kiørboe T (1993) Turbulence, phytoplankton cell size, and the structure of pelagic food webs. Advances in Marine Biology 29: 2-72

Kiørboe T, Hansen JLS (1993) Phytoplankton aggregate formation: observations of patterns and mechanisms of cell sticking and the significance of exopolymeric material. Journal of Plankton Research 15: 993-1018

Kirkwood JM (1993) Zooplankton community dynamics and diel vertical migration in Ellis Fjord, Vestfold Hills Antarctica. PhD thesis, Monash University, Melbourne, 351 pp

Kirkwood JM, Burton HR (1987) Three new zooplankton nets designed for under-ice sampling; with preliminary results of collections made from Ellis fjord, Antarctica during 1985. Proceedings NIPR Symposium Polar Biology 1: 112-122

Kirkwood JM, Burton HR (1988) Macrobenthic species assemblages in Ellis Fjord, Vestfold Hills, Antarctica. Marine Biology 97: 445-457

Klaas C (1997a) Distribution and role of microprotozoa in the Southern Ocean. Berichte zur Polarforschung 253: 119 pp

Klaas C (1997b) Microprotozooplankton distribution and their potential grazing in the Antarctic Circumpolar Current. Deep-Sea Research II 44: 375-393

Klein Breteler WCM, Schogt N, Baas M, Schouten S, Kraay GW (1999) Trophic upgrading of food quality by protozoans enhancing copepod growth: role of essential lipids. Marine Biology 135: 191-198

Knauer GA, Karl DM, Martin JH, Hunter CN (1984) *In situ* effects of selected preservatives on total carbon, nitrogen and metals collected in sediment traps. Journal of Marine Research 42: 445-462

Kopczynska EE, Goeyens L, Semeneh M, Dehairs F (1995) Phytoplankton composition and cell carbon distribution in Prydz Bay, Antarctica: relation to organic particulate matter and its delta ^{13}C values. Journal of Plankton Research 17: 685-707

Kottmeier ST, Sullivan CW (1987) Late winter primary production and bacterial production in sea ice and seawater west of the Antarctic peninsula. Marine Ecology Progress Series 36: 287-298

Kottmeier ST, Sullivan CW (1990) Bacterial biomass and production in pack ice of Antarctic marginal ice edge zones. Deep-Sea Research 37: 1311-1330

Krebs WN (1983) Ecology of neritic marine diatoms, Arthur Harbor, Antarctica. Micropaleontology 29: 267-297

Kruskal JB, Wish M (1978) Multidimensional Scaling. In JL Sullivan (ed) Quantitative Applications in the Social Sciences. SAGE Publications, Beverly Hills 93 pp

Lampert W (1978) Release of dissolved organic carbon by grazing zooplankton. Limnology and Oceanography 23: 831-834

Lampitt RS, Noji T, von Bodungen B (1990) What happens to zooplankton faecal pellets? Implications for material flux. Marine Biology 104: 15-23

Lancelot C, Becquevort S, Menon P, Mathot S, Dandois J-M (1997) Ecological modelling of the planktonic microbial food-web. Universite Libre de Bruxelles Groupe de Microbiologie des Milieux Aquatiques, Brussels, 78 pp

Lancelot C, Mathot S, Veth C, de Baar H (1993) Factors controlling phytoplankton ice-edge blooms in the marginal ice-zone of the norethwestern Weddell Sea during sea ice retreat 1988: field observations and mathematical modelling. Polar Biology 13: 377-387

Lane PVZ, Smith SL, Urban JL, Biscaye PE (1994) Carbon flux and recycling associated with zooplanktonic fecal pellets on the shelf of the Middle Atlantic Bight. Deep-Sea Research 41: 437-457

Leakey RJG, Burkill PH, Sleigh MA (1994) A comparison of fixatives for the estimation of abundance and biovolume of marine planktonic ciliate populations. J Plankton Res 16: 375-389

Leakey RJG, Archer SD, Grey J (1996) Microbial dynamics in coastal waters of eastern Antarctica: bacterial production and nanoflagellate herbivory. Mar Ecol Prog Ser 142: 3-17

Le Fèvre J, Legendre L, Rivkin RB (1998) Fluxes of biogenic carbon in the Southern Ocean: roles of large microphagous zooplankton. Journal of Marine Systems 17: 325-345

Lee C (1990). Technical problems with the use of sediment traps - preservation, swimmers and leaching. Paper presented at the Sediment traps in marine ecological research and monitoring, Kristineberg Marine Biological Station, Fiskebackskil, Sweden, p 36-48

Lee C, Hedges JI, Wakeham SG, Zhu N (1992) Effectiveness of various treatments in retarding microbial activity in sediment trap material and their effects on the collection of swimmers. Limnology and Oceanography 37: 117-130

Leech DM, Williamson CE (2000) Is tolerance to UV radiation in zooplankton related to body size, taxon, or lake transparency? Ecological Applications 10: 1520-1540

Legendre L, Le Fèvre J (1989) Hydrodynamical singularities as controls of recycled versus export production in oceans. In WH Berger, VS Smetacek, G Wefer (eds) Productivity of the ocean: present and past. John Wiley Sons Ltd., Chichester, p 49-63

Legendre L, Rassoulzadegan F (1996) Food-web mediated export of biogenic carbon in oceans: hydrodynamical control. Marine Ecology Progress Series 145: 179-193

Lessard EJ (1991) The trophic role of heterotrophic dinoflagellates in diverse marine environments. Marine Microbial Food Webs 5: 49-58

Lessard EJ, Rivkin RB (1986) Nutrition of microzooplankton and macrozooplankton from McMurdo Sound. Antarctic Journal of the U.S. 21: 187-188

Leventer A (1991) Sediment trap diatom assemblages from the northern Antarctic Peninsula region. Deep-Sea Research 38: 1127-1143

Levinsen H, Turner JT, Nielsen TG, Hansen BW (2000) On the trophic coupling between protists and copepods in arctic marine ecosystems. Marine Ecology Progress Series 204: 65-77

Longhurst AR (1991) Role of the marine biosphere in the global carbon cycle. Limnology and Oceanography 36: 1507-1526

Longhurst AR, Harrison WG (1989) The biological pump: profiles of plankton production and consumption in the upper ocean. Progress in Oceanography 22: 47-123

Lonsdale DJ, Caron DA, Dennett MR, Schaffner R (2000) Predation by *Oithona* spp. on protozooplankton in the Ross Sea, Antarctica. Deep-Sea Research II 47: 3273-3283

Lutter S, Taasen JP, Hopkins CCE, Smetacek V (1989) Phytoplankton dynamics and sedimentation processes during spring and summer in Balsfjord, Northern Norway. Polar Biology 10: 113-124

Madin LP (1982) Production, composition and sedimentation of salp fecal pellets in oceanic waters. Marine Biology 67: 39-45

Marchant HJ, Davidson AT, Wright SW (2001) Antarctic marine microorganisms and climate change: impacts and feedbacks. Ocean and Polar Research 23: 401-410

Marchant HJ, Murphy EJ (1994) Interactions at the base of the Antarctic food web. In SZ El-Sayed (ed) Southern Ocean Ecology: The BIOMASS Perspective. Cambridge University Press, Cambridge, p 267-280

Marchant HJ, Thomas DP (1983) Polylysine as an adhesive for the attachment of nanoplankton to substrates for electron microscopy. Journal of Microscopy 131: 127-129

Marchant HJ, Watanabe K, Kawachi M (1996) Marine snow in Antarctic coastal waters. Proceedings of the NIPR Symposium Polar Biology 9: 75-83

Marshall SM, Orr AP (1955) The Biology of a Marine Copepod *Calanus finmarchicus* (Gunnerus). Oliver Boyd, London, 195 pp

Martens P (1978) Faecal pellets. Fiches D'Identification du Zooplancton 162: 4 pp.

Martens P, Krause M (1990) The fate of faecal pellets in the North Sea. Helgolander Meeresunters 44: 9-19

Mathot S, Dandois J-M, Lancelot C (1992) Gross and net primary production in the Scotia-Weddell Sea sector of the Southern Ocean during spring 1988. Polar Biol. 12: 321-332

Matsuda O, Ishikawa S, Kawaguchi K (1987) Seasonal variation of downward flux of particulate organic matter under the Antarctic fast ice. Proceedings of the NIPR Symposium Polar Biology 1: 23-34

Matsuda O, Ishikawa S, Kawaguchi K (1990) Seasonal variation of particulate organic matter under the Antarctic fast ice and its importance to benthic life. In KR Kerry, G Hempel (eds) Antarctic Ecosystems: Ecological change and conservation. Springer-Verlag Berlin, Heidelberg, p 143-148

McMinn A (1994) Preliminary investigation of a method for determining past winter tempereatures at Ellis Fjord, eastern Antarctica, from fast ice assemblages. Memoirs of the Japanese Institute for Polar Research, Special Issue 50: 34-40

McMinn A (1996) Preliminary investigation of the contribution of fast-ice algae to the spring phytoplankton bloom in Ellis Fjord, eastern Antarctica. Polar Biology 16: 301-307

McMinn A, Bleakley N, Steinburner K, Roberts D, Trenerry L (2000) Effect of permanent sea ice cover and different nutrient regimes on the phytoplankton succession of fjords of the Vestfold Hills Oasis, eastern Antarctica. Journal of Plankton Research 22: 287-303

McMinn A, Gibson J, Hodgson D, Aschman J (1995) Nutrient limitation in Ellis Fjord, eastern Antarctica. Polar Biology 15: 269-276

McMinn A, Hodgson D (1993) Summer phytoplankton succession in Ellis Fjord, eastern Antarctica. Journal of Plankton Research 15: 925-938

Medlin LK, Priddle J (1990) Polar Marine Diatoms. British Antarctic Survey, Cambridge

Menden-Deuer S, Lessard EJ (2000) Carbon to volume relationships for dinoflagellates, diatoms, and other protist plankton. Limnology and Oceanography 45: 569-579

Menden-Deuer S, Lessard EJ, Satterberg J (2001) Effect of preservation on dinoflagellate and diatom cell volume and consequences for carbon biomass predictions. Marine Ecology Progress Series 222: 41-50

Metz C (1995) Seasonal variation in the distribution and abundance of *Oithona* and *Oncaea* species (Copepoda, Crustacea) in the southeastern Weddell Sea, Antarctica. Polar Biol 15: 187-194

Metz C (1996) Life strategies of dominant Antarctic Oithonidae (Cyclopoida, Copepoda) and Oncaeidae (Poecilostomatoida, Copepoda) in the Bellingshausen Sea. Alfred-Wegener Institute fur Polar-und Meeresforschung, Bremerhaven

Metz C (1998) Feeding of *Oncaea curvata* (Poecilostomatoida, Copepoda). Marine Ecology Progress Series 169: 229-235

Michaels AF, Silver MW (1988) Primary production, sinking fluxes and the microbial food web. Deep-Sea Research 35: 473-490

Michaels AF, Silver MW, Gowing MM, Knauer GA (1990) Cryptic zooplankton "swimmers" in upper ocean sediment traps. Deep-Sea Research 37: 1285-1296

Michel C, Legendre L, Taguchi S (1997) Coexistence of microalgal sedimentation and water column recycling in a seasonally ice-covered ecosystem (Saroma-ko Lagoon, Sea of Okhotsk, Japan). Journal of Marine Systems 11: 133-148

Mills CE (1995) Medusae, siphonophores, and ctenophores as planktivorous predators in changing global ecosystems. ICES Journal of Marine Science 52: 575-581

Moline MA, Prezelin BB (1996) Long-term monitoring and analyses of physical factors regulating variability in coastal Antarctic phytoplankton biomass, *in situ* productivity and taxonomic composition over subseasonal, seasonal and interannual time scales. Marine Ecology Progress Series 145: 143-160

Moline MA, Prezelin BB (2000) Optical fractionation of chlorophyll and primary production for coastal waters of the Southern Ocean. Polar Biol. 23: 129-136

Moline MA, Prezelin BB, Schofield O, Smith RC (1997) Temporal dynamics of coastal Antarctic phytoplankton: environmental driving forces and impact of a 1991/92 summer diatom bloom on the nutrient regimes. In B Battaglia, J Valencia, DWH Walton (eds) Antarctic communities: species structure and survival. Cambridge University Press, Cambridge, p 67-72

Montressor M, Procaccini G, Stoecker DK (1999) *Polarella glacialis*, Gen. Nov., Sp. Nov. (Dinophyceae): Suessiaceae are still alive! Journal of Phycology 35: 186-197

Morales CE, Harris RP, Head RN, Tranter PRG (1993) Copepod grazing in the oceanic northeast Atlantic during a 6 week drifting station: the contribution of size classes and vertical migrants. Journal of Plankton Research 15: 185-211

Müller H (2002) Laboratory study of the life cycle of a freshwater strombidiid ciliate. Aquatic Microbial Ecology 29: 189-197

MZC2 (2001) Future marine zooplankton research - a perspective. Marine Ecology Progress Series 222: 297-308

Naes K (1988) Effect of additives on organic break down in sediment traps: preliminary results. In P Wassmann, A-S Heiskanen (eds) Sediment trap studies in the Nordic countries 1, Yliopistopaino, Helsinki, p 38-43

Nakamura Y, Turner JT (1997) Predation and respiration by the small cyclopoid copepod *Oithona similis*: How important is feeding on ciliates and heterotrophic flagellates? Journal of Plankton Research 19: 1275-1288

Nelson DM, DeMaster DJ, Dunbar RB, Smith Jr. WO (1996) Cycling of organic carbon and biogenic silica in the Southern Ocean: Estimates of water-column and sedimentary fluxes on the Ross Sea continental shelf. Journal of Geophysical Research 101: 18, 519 - 18, 532

Nelson JR (1989) Phytoplankton pigments in macrozooplankton feces: variability in carotenoid alterations. Marine Ecology Progress Series 52: 129-144

Newman SJ, Nicol S, Ritz D, Marchant H (1999) Susceptibility of Antarctic krill (*Euphausia superba* Dana) to ultraviolet radiation. Polar Biology 22: 50-55

Nicol S, Stolp M (1989) Sinking rates of cast exoskeletons of Antarctic krill (*Euphausia superba* Dana) and their role in the vertical flux of particulate matter and fluoride in the Southern Ocean. Deep-Sea Research 36: 1753-1762

Nielsen TG, Lokkegaard B, Richardson K, Pedersen FB, Hansen L (1993) Structure of plankton communities in the Dogger Bank area (North Sea) during a stratified situation. Marine Ecology Progress Series 95: 115-131

Nielsen TG, Sabatini M (1996) Role of cyclopoid copepods *Oithona* spp. in North Sea plankton communities. Marine Ecology Progress Series 139: 79-93

Nodder SD, Alexander BL (1999) The effects of multiple trap spacing, baffles and brine volume on sediment trap collection efficiency. Journal of Marine Research 57: 537-559

Noji T (1991) The influence of macrozooplankton on vertical particulate flux. Sarsia 76: 1-9

Noji TT, Estep KW, MacIntyre F, Norrbin F (1991) Image analysis of faecal material grazed upon by three species of copepods: evidence for coprorhexy, coprophagy and coprochaly. Journal of the Marine Biological Association of the U.K. 71: 465-480

Nöthig A-M (1988) On the ecology of the phytoplankton in the southeastern Weddell Sea (Antarctica) in January/February 1985. Berichte Polarforschung 53: 1-118

Nöthig EM, von Bodungen B (1989) Occurrence and vertical flux of faecal pellets of probably protozoan origin in the southeastern Weddell Sea (Antarctica). Marine Ecology Progress Series 56: 281-289

Nöthig E-M, von Bodungen B, Sui Q (1991) Phyto- and protozooplankton biomass during austral summer in surface waters of the Weddell Sea and vicinity. Polar Biology 11: 293-304

Ohman MD, Snyder RA (1991) Growth kinetics of the omnivorous oligotroch ciliate, *Strombidium* sp. Limnology and Oceanography 36: 922-935

Ohtsuka S, Kubo N (1991) Larvaceans and their houses as important food for some pelagic copepods. Proceedings of the Fourth International Conference on Copepoda, Bulletin of the Plankton Society Japan. Special volume p 535-551

Olesen M (2001) Sedimentation in Mariager Fjord, Denmark: the impact of sinking velocity on system productivity. Ophelia 55: 11-26

Omori M, Ikeda T (1984) Methods in Marine Zooplankton Ecology. John Wiley and Sons, New York, 332 pp

Pace ML, Orcutt J, J.D. (1981) The relative importance of protozoans, rotifers, and crustaceans in a freshwater zooplankton community. Limnology and Oceanography 26: 822-830

Paffenhöfer G-A (1976) Feeding, growth, and food conversion of the marine planktonic copepod *Calanus helgolandicus*. Limnology and Oceanography 21: 39-50

Paffenhöfer G-A (1993) On the ecology of marine cyclopoid copepods (Crustacea, Copepoda). Journal of Plankton Research 15: 37-55

Paffenhöfer G-A (1998) Heterotrophic protozoa and small metazoa: feeding rates and prey-consumer interactions. Journal of Plankton Research 20: 121-133

Pakhomov Y (1993) Feeding habits and estimate of ration of Gray Notothenia, *Notothenia squamifrons squamifrons*, on the Ob and Lena tablemounts (Indian sector of Antarctica). Journal of Icthyology 33: 57-71

Palmisano AC, Sullivan CW (1983) Sea ice microbial communities (SIMCO) 1. Distribution, abundance and primary production of ice microalgae in McMurdo Sound, Antarctica in 1980. Polar Biology 2: 171-177

Parsons TR, Maita Y, Lalli CM (1984) A manual of chemical and biological methods for seawater analysis. Pergamon Press, Oxford 173 pp

Pasternak A, Arashkevich E, Wexels Riser CW, Ratkova T, Wassmann P (2000) Seasonal variation in zooplankton and suspended faecal pellets in the subarctic Norwegian Balsfjorden, in 1996. Sarsia: 439-452

Patterson DJ, Nygaard K, Steinberg G, Turley CM (1993) Heterotrophic flagellates and other protists associated with oceanic detritus throughout the water column in the mid North Atlantic. Journal of the Marine Biological Association UK 73: 67-95

Pearse JS, Bosch I, Pearse VB, Basch LV (1991) Reproduction of Antarctic benthic marine invertebrates: tempos, modes and timing. American Zoologist 31: 65-80

Pearse JS, Giese AC (1966) Food, reproduction and organic constitution of the common Antarctic echinoid *Sterechinus neumayerii*(Meissner). Biological Bulletin 130: 387-401

Peinert R, Saure A, Stegmann P, Stienen C, Haardt H, Smetacek V (1982) Dynamics of primary production and sedimentation in a coastal ecosystem. Netherlands Journal of Sea Research 16: 276-289

Peinert R, von Bodungen B, Smetacek VS (1989) Food web structure and loss rate. In WH Berger, VS Smetacek, G Wefer (eds) Productivity of the ocean: present and past. John Wiley Sons Ltd., Chichester, p 35-48

Perrin RA, Lu P, Marchant HJ (1987) Seasonal variation in marine phytoplankton and ice algae at a shallow antarctic coastal site. Hydrobiologia 146: 33-46

Pesant S, Legendre L, Gosselin M, Ashjian C, Booth B, Daly K, Fortier L, Hirche H-J, Michaud J, Smith REH, Smith S, Smith Jr. WO (1998) Pathways of carbon cycling in the euphotic zone: the fate of large-sized phytoplankton in the Northeast Water Polynya. Journal of Plankton Research 20: 1267-1291

Peterson ML, Hernes PJ, Thoreson DS, Hedges JI, Lee C, Wakeham SG (1993) Field evaluation of a valved sediment trap. Limnology and Oceanography 38: 1741-1761

Peterson W, Dam HG (1990) The influence of copepod "swimmers" on pigment fluxes in brine-filled vs. ambient seawater-filled sediment traps. Limnology and Oceanography 35: 448-455

Pierce RW, Turner JT (1992) Ecology of planktonic ciliates in marine food webs. Reviews in Aquatic Sciences 6: 139-181

Pusceddu A, Cattaneao-Vietti R, Albertelli G, Fabiano M (1999) Origin, biochemical composition and vertical flux of particulate organic matter under the pack ice in Terra Nova Bay (Ross Sea, Antarctica) during late summer 1995. Polar Biology 22: 124-132

Quetin LB, Ross RM (1985) Feeding by Antarctic krill, *Euphausia superba*: Does size matter? In WR Siegfried, PR Condy, RM Laws (eds.), Antarctic Nutrient Cycles and Food Webs. Springer-Verlag, Berlin, p 373-377

Rautio M, Korhola A (2002) Effects of ultraviolet radiation and dissolved organic carbon on the survival of subarctic zooplankton. Polar Biology 25: 460-468

Razouls S, Reau GD, Guillot P, Maison J, Jeandel C (1998) Seasonal abundance of copepod assemblages and grazing pressure in the Kerguelen Island area (Southern Ocean). Journal of Plankton Research 20: 1599-1614

Reeve MR, Walter MA (1978) Nutritional ecology of ctenophores - a review of recent research. Advances in Marine Biology 15: 249-287

Reigstad M, Wassmann P, Ratkova T, Arashkevich E, Pasternak A, Oygarden S (2000) Comparison of the springtime vertical export of biogenic matter in three northern Norwegian fjords. Marine Ecology Progress Series 201: 73-89

Riebesell U (1991) Particle aggregation during a diatom bloom. II. Biological aspects. Marine Ecology Progress Series 69: 281-291

Riebesell U, Reigstad M, Wassmann P, Noji T, Passow U (1995) On the trophic fate of *Phaeocystis pouchetii* (Hariot): VI Significance of *Phaeocystis*-derived mucus for vertical flux. Netherlands Journal of Sea Research 33: 193-203

Riebesell U, Schloss I, Smetacek V (1991) Aggregation of algae released from melting sea ice: implications for seeding and sedimentation. Polar Biology 11: 239-248

Rivkin RB, Bosch I, Pearse JS, Lessard EJ (1986) Bacteriovory: a novel feeding mode for Asteroid larvae. Science 233: 1311-1314

Rivkin RB, Legendre L (2001) Biogenic carbon cycling in the upper ocean: effects of microbial respiration. Science 291: 2398-2400

Rivkin RB, Legendre L, Deibel D, Tremblay J-E, Klein Breteler WCM, Crocker K, Roy S, Silverberg N, Lovejoy C, Mesple F, Romero N, Anderson MR, Matthews P, Savenkoff C, Vézina A, Therriault J-C, Wesson J, Berube C, Ingram RG (1996) Vertical flux of biogenic carbon in the ocean: is there food web control? Science 272: 1163-1166

Rodriguez J, Tintore J, Allen JT, Blanco JM, Gomis D, Reul A, Ruiz J, Rodriguez V, Echevarria F, Jimenez-Gomez F (2001) Mesoscale vertical motion and the size structure of phytoplankton in the ocean. Nature 410: 360-363

Roman MR, Ducklow HW, Fuhrman JA, Garside C, Glibert PM, Malone TC, McManus GB (1988) Production, consumption and nutrient cycling in a laboratory mesocosm. Marine Ecology Progress Series 42: 39-52

Rosa F, Bloesch J, Rathke DE (1994) Sampling the settling and suspended particulate matter (SPM). In A Murdoch SD MacKnight (eds) Handbook of techniques for aquatic sediments sampling. Lewis Publishers, Boca Raton, 236 pp

Roy S, Harris RP, Poulet SA (1989) Inefficient feeding by *Calanus helgolandicus* and *Temora longicornsis* on *Coscinodiscus wailesii*: quantitative estimation using chlorophyll-type pigments and effects on dissolved free amino acids. Marine Ecology Progress Series 52: 145-153

Sabatini M, Kiørboe T (1994) Egg production, growth and development of the cyclopoid copepod *Oithona similis*. Journal of Plankton Research 16: 1329-1351

Saggiomo V, Carrada GC, Mangoni O, Ribera d'Alcala M, Russo A (1998) Spatial and temporal variability of size-fractionated biomass and primary production in the Ross Sea (Antarctica) during austral spring and summer. Journal of Marine Systems 17: 115-127

Saggiomo V, Catalano G, Mangoni O, Budillon G, Carrada GC (2002) Primary production processes in ice-free waters of the Ross Sea (Antarctica) during the austral summer 1996. Deep-Sea Research 49: 1787-1801

Saito R, Kudoh S, Sato T, Watanabe K, Fukuchi M (1998) Composition of sinking particulates collected under fast ice near Syowa station, East Antarctica, in early spring and early summer, 1994. Antarctic Record 42: 252-268

Sanders RW, Wickham SA (1993) Planktonic protozoa and metazoa: predation, food quality and population control. Marine Microbial Food Webs 7: 197-223

Sarmiento JL, Le Quere C (1996) Oceanic carbon dioxide uptake in a model of century-scale global warming. Science 274: 1346-1350

Sasaki H, Hoshiai T (1986) Sedimentation of microalgae under the Antarctic fast ice in summer. Memoirs of the National Institute of Polar Research Special Issue 40: 45-55

Schloss IR, Ferreyra GA, Mercuri G, Kowalke J (1999) Particle flux in an Antarctic shallow coastal environment: a sediment trap study. Scientia Marina 63: 99-111

Schnack SB, Marschall S, Mizdalski E (1985) On the distribution of copepods and larvae of *Euphausia superba* in Antarctic waters during February 1982. Meeresforschung 30: 251-263

Schnack-Schiel SB, Hagen W, Mizdalski E (1998b) Seasonal carbon distribution of copepods in the eastern Weddell Sea, Antarctica. Journal of Marine Systems 17: 305-311

Schnack-Schiel SB, Thomas D, Dahms H-U, Haas C, Mizdalski E (1998a) Copepods in Antarctic Sea-ice. Antarctic Sea Ice Biological Processes, Interactions, and Variability Antarctic Research Series 73: 173-182

Schnack-Schiel SB, Thomas DN, Haas C, Dieckmann GS, Alheit R (2001) The occurrence of the copepods *Stephos longipes* (Calanoida) and *Drescheriella glacialis* (Harpacticoida) in summer sea ice in the Weddell Sea, Antarctica. Antarctic Science 13: 150-157

Schnepf E, Elbrächter M (1992) Nutritional strategies in dinoflagellates: a review with emphasis on cell biological aspects. European Journal of Protistology 28: 3-24

Scott JM (1985) The feeding rates and efficiencies of a marine ciliate, *Strombidium* sp., grown under chemostat steady-state conditions. Journal of Experimental Marine Biology and Ecology 90: 81-95

Serret P, Fernandez E, Anadón R, Varela M (2001) Trophic control of biogenic carbon export in Bransfield and Gerlache Straits, Antarctica. Journal of Plankton Research 12: 1345-1360

Sherr E, Sherr B (1988) Role of microbes in pelagic food webs: A revised concept. Limnology and Ocenaography 33: 1225-1227

Sherr EB, Sherr BF (1993) Preservation and storage of samples for enumeration of heterotrophic protists. In PF Kemp, BF Sherr, EB Sherr, JJ Cole (eds) Handbook of methods in aquatic microbial ecology. Lewis Publishers, Boca Raton, p 229-242

Sherr EB, Sherr BF, Paffenhöfer G-A (1986) Phagotrophic protozoa as food for metazoans: a "missing" trophic link in marine pelagic food webs? Marine Microbial Food Webs 1: 61-80

Siegenthaler U, Sarmiento JL (1993) Atmospheric carbon dioxide and the ocean. Nature 365: 119-125

Silver MW, Gowing MM (1991) The "particle" flux: origins and biological components. Progress in Oceanography 26: 75-113

Silver MW, Shanks AL, Trent JD (1978) Marine snow: microzooplankton habitat and source of small-scale patchiness in pelagic populations. Science 201: 371-373

Small LF, Knauer GF, Tuel MD (1987) The role of sinking fecal pellets in stratified euphotic zones. Deep-Sea Research 34: 1705-1712

Smayda TJ (1970) The suspension and sinking of phytoplankton in the sea. Oceanography and Marine Biology An Annual Review 8: 353-414

Smetacek V (1985) Role of sinking in diatom life-history cycles: ecological, evolutionary and geological significance. Marine Biology 84: 239-251

Smetacek V (2000) The giant diatom pump. Nature 406: 574-575

Smetacek V, Scharek R, Nöthig E-M (1990) Seasonal and regional variation in the pelagial and its relationship to the life history cycle of krill. In KR Kerry, G Hempel (eds) Antarctic Ecosystems: ecological change and conservation. Springer-Verlag berlin, Heidelberg, p 103-114

Smetacek VS (1980) Zooplankton standing stock, copepod faecal pellets and particulate detritus in Kiel Bight. Estuarine and Coastal Marine Science 11: 477-490

Smith N, Tréguer P (1994) Physical and chemical oceanography in the vicinity of Prydz Bay, Antarctica. In SZ El-Sayed (ed) Southern Ocean Ecology: The BIOMASS Perspective. Cambridge University Press, Cambridge, p 25-43

Smith Jr WO, Nelson DM (1986) Importance of ice edge phytoplankton production in the Southern Ocean. Bioscience 36: 251-257

Socal G, Nöthig EM, Bianchi F, Boldrin A, Mathot S, Rabitti S (1997) Phytoplankton and particulate matter at the Weddell / Scotia confluence (47°W) in summer 1989, as a final step of a temporal succession (EPOS project). Polar Biology 18: 1-9

Stanwell-Smith D, Peck LS (1998) Temperature and embryonic development in relation to spawning and field occurrence of larvae of three Antarctic echinoderms. Biological Bulletin 194: 44-52

Stanwell-Smith D, Peck LS, Clarke A, Murray AWA, Todd CD (1999) The distribution, abundance and seasonality of pelagic marine invertebrate larvae in the maritime Antarctic. Philosophical Transactions of the Royal Society London B 354: 471-484

Statsoft Inc. (2001) STATISTICA ©, (data analysis software system), version 6. www.statsoft.com

Steedman HFE (1976) Zooplankton fixation and preservation. The Unesco Press, Paris, 350 pp

Steinberg DK, Pilskaln CH, Silver MW (1998) Contribution of zooplankton associated with detritus to sediment trap 'swimmer' carbon in Monterey Bay, California, USA. Marine Ecology Progress Series 164: 157-166

Stoecker DK (1984) Particle production by planktonic ciliates. Limnology and Oceanography 29: 930-940

Stoecker DK, Buck KR, Putt M (1990) A flagellate- and ciliate- dominated microbial community in the land-fast ice. Antarctic Journal of the U.S. 25: 197-199

Stoecker DK, Buck KR, Putt M (1991) Photosynthetic dinoflagellates and their cysts characteristic of the land-fast ice. Antarctic Journal of the U.S. 26: 143-144

Stoecker DK, Buck KR, Putt M (1992) Changes in the sea-ice brine community during the spring-summer transition, McMurdo Sound, Antarctica I. Photosynthetic protists. Marine Ecology Progress Series 84: 265-278

Stoecker DK, Buck KR, Putt M (1993) Changes in the sea-ice brine community during the spring-summer transition, McMurdo Sound, Antarctic. II. Phagotrophic protists. Marine Ecology Progress Series 95: 103-113

Stoecker DK, Capuzzo JM (1990) Predation on protozoa: its importance to zooplankton. Journal of Plankton Research 12: 891-908

Straile D (1997) Gross growth efficiencies of protozoan and metazoan zooplankton and their dependence on food concentration, predator-prey weight ratio, and taxonomic group. Limnology and Oceanography 42: 1375-1385

Strathmann RR (1967) Estimating the organic carbon content of phytoplankton from cell volume or plasma volume. Limnology and Oceanography 12: 411-418

Strathmann RR (1971) The feeding behaviour of planktotrophic echinoderm larvae: mechanisms, regulation, and rates of suspension-feeding. Journal of Experimental Marine Biology and Ecology 6: 109-160

Strom SL (1991) Growth and grazing rates of the herbivorous dinoflagellate *Gymnodinium* sp. from the open subarctic Pacific Ocean. Mar Ecol Prog Ser 78: 103-113

Strom SL, Benner R, Ziegler S, Dagg MJ (1997) Planktonic grazers are a potentially important source of marine dissolved organic carbon. Limnology and Oceanography 42: 1364-1374

Suzuki H, Sasaki H, Fukuchi M (2001) Short-term variability in the flux of rapidly sinking particles in the Antarctic marginal ice zone. Polar Biology 24: 697-705

Swadling KM (2001) Population structure of two Antarctic ice-associated copepods, *Drescheriella glacialis* and *Paralabidocera antarctica*, in winter sea ice. Marine Biology

Swadling KM (1998) Influence of Seasonal Ice Formation on Life Cycle Strategies of Antarctic Copepods. PhD thesis, University of Tasmania, Hobart, 217 pp

Swadling KM, Gibson JAE, Ritz DA, Nichols PD, Hughes DE (1997) Grazing of phytoplankton by copepods in eastern Antarctic coastal waters. Marine Biology 128: 39-48

Swadling KM, McKinnon D (in prep) Growth, production and life cycle plasticity of the copepod *Paralabidocera antarctica* in east Antarctica.

Swadling KM, McPhee AD, McMinn A (2000a) Spatial distribution of copepods in fast ice of eastern Antarctica. Polar Bioscience 13: 55-65

Swadling KM, Nichols PD, Gibson JAE, Ritz DA (2000b) Role of lipid in the life cycles of ice-dependent and ice-independent populations of the copepod *Paralabidocera antarctica*. Marine Ecology Progress Series 208: 171-182

Syvitski JPM, Burrell DC, Skei JM (1987) Fjords: processes and products. Springer-Verlag, New York 379 pp

Taguchi S, Hargrave BT (1978) Loss rates of suspended material sedimented in a marine bay. Journal of the Fisheries Research Board Canada 35: 1614-1620

Tanimura A, Fukuchi M, Hoshiai T (1986) Seasonal change in the abundance of zooplankton and species composition of copepods in the ice-covered sea near Syowa station, Antarctica. Memoirs of the National Institute of Polar Research Special Issue 40: 212-220

Tanimura A, Hoshino K, Nonaka Y, Miyamoto Y, Hattori H (1997) Vertical distribution of *Oithona similis* and *Oncaea curvata* (Cylcopoida, Copepoda) under sea ice near Syowa Station in the Antarctic winter. Proceedings of the NIPR Symposium on Polar Biology 10: 134-144

Tanimura A, Hoshia T, Fukuchi M (1996) The life cycle strategy of the ice-associated copepod, *Paralabidocera antarctica* (Calanoida, Copepoda), at Syowa Station, Antarctica. Antarctic Science 8: 257-266

Tanimura A, Minoda T, Fukuchi M, Hoshiai T, Ohtsuka H (1984) Swarm of *Paralabidocera antarctica* (Calanoida, Copepoda) under sea ice near Syowa Station, Antarctica. Nanyoku Shiryo (Antarctic Record) 82: 12-19

Taylor GT, Karl DM, Pace ML (1986) Impact of bacteria and zooflagellates on the composition of sinking particles: an *in situ* experiment. Marine Ecology Progress Series 29: 141-155

Thomson P (2000) Ecophysiology of the brine dinoflagellate, *Polarella glacialis*, and Antarctic fast ice brine communities. PhD thesis University of Tasmania, Hobart 175 pp

Tian RC, Vézina AF, Starr M, Saucier F (2001) Seasonal dynamics of coastal ecosystems and export production at high latitudes: a modeling study. Limnology and Oceanography 46: 1845-1859

Tomas CRE (1996) Identifying marine diatoms and dinoflagellates. Academic Press, California, 598 pp

Tréguer P (1994) The Southern Ocean: biogeochemical cycles and climate changes. In G Hempel (ed) Antarctic Science: global concerns. Springer-Verlag, Berlin Heidelberg, p 110-125

Trull TW, Gibson JAE, Beaumont KL, Bowman J, Burton HR, Davidson AT, Guichard A, Kirkwood JM, McMinn A, Nichols PD, Skerratt JH, Summons RE, Swadling KM, Volkman JK (2001) Site holds promise for ecosystem and biogeochemical investigations. Eos, Transactions, American Geophysical Union 82: 306,311

Tsuda A, Kawaguchi S (1997) Microzooplankton grazing in the surface water of the Southern Ocean during an austral summer. Polar Biology 18: 240-245

Tucker MJ (1983) The zooplankton and ice-water interface fauna of the inshore marine are of the Vestfold Hills, Antarctica. BSc (Hons) thesis, University of Tasmania, Hobart, 158 pp

Tucker MJ, Burton HR (1990) Seasonal and spatial variation in the zooplankton community of an eastern Antarctic coastal location. Polar Biology 10: 571-579

Turner JT (1984) Zooplankton feeding ecology : contents of fecal pellets of the copepods *Temora turbinata* and *T. stylifera* from continental shelf and slope waters near the mouth of the Mississippi RIver. Marine Biology 82: 73-83

Turner JT (2000) Feeding ecology of marine copepods: an overview of recent studies and emerging issues. National Taiwan Museum Special Publication Series. Proceedings of the International Symposium on Marine Biology in Taiwan - Crustacean and Zooplankton Taxonomy, Ecology and Living Resources, 26-27 May, 1998, Taiwan 10: 37-57

Turner JT (2002) Zooplankton fecal pellets, marine snow and sinking phytoplankton blooms. Aquatic Microbial Ecology 27: 57-102

Turner JT, Ferrante JG (1979) Zooplankton fecal pellets in aquatic ecosystems. Bioscience 29: 670-677

Turner JT, Granéli E (1992) Zooplankton feeding ecology: grazing during enclosure studies of phytoplankton blooms from the west coast of Sweden. Journal of Experimental Marine Biology and Ecology 157: 19-31

Umani SF, Monti M, Nuccio C (1998) Microzooplankton biomass distribution in Terra Nova Bay, Ross Sea (Antarctica). Journal of Marine Systems 17: 298-303

Urban-Rich J (2001) Seston effects on faecal pellet carbon concentrations from a mixed community of copepods in Balsfjord, Norway, and the Antarctic Polar Front. ICES Journal of Marine Science 58: 700-710

Urban-Rich J, Dagg M, Peterson J (2001) Copepod grazing on phytoplankton in the Pacific sector of the Antarctic Polar Front. Deep-Sea Research 48: 4223-4246

Urban-Rich JL, Hansell DA, Roman MR (1998) Analysis of copepod fecal pellet carbon using a high temperature combustion method. Mar Ecol Prog Ser 171: 199-208

Urban-Rich J, Nordby E, Andreassen IJ, Wassmann P (1999) Contribution by mesozooplankton fecal pellets to the carbon flux on Nordvestbanken, north Norwegian shelf in 1994. Sarsia 84: 253-264

Urban-Rich JL (1997) Latitudinal variations in the contribution by copepod fecal pellets to organic carbon and amino acid flux. PhD thesis, University of Maryland, 188 pp

Urrere MA, Knauer GA (1981) Zooplankton fecal pellet fluxes and vertical transport of particulate organic material in the pelagic environment. Journal of Plankton Research 3: 369-387

Verity P, Smetacek V (1996) Organism life cycles, predation, and the structure of marine pelagic ecosystems. Marine Ecology Progress Series 130: 277-293

Verity PG (1985) Grazing, respiration, excretion, and growth rates of tintinnids. Limnology and Oceanography 30: 1268-1282

Verity PG, Vernet M (1992) Microzooplankton grazing, pigments, and composition of plankton communities during late spring in two Norwegian fjords. Sarsia 77: 263-274

Vézina AF, Platt T (1988) Food web dynamics in the ocean. I. Best-estimates of flow networks using inverse methods. Marine Ecology Progress Series 42: 269-287

Viitasalo M, Rosenberg M, Heiskanen A-S, Kosi M (1999) Sedimentation of copepod fecal material in the coastal northern Baltic Sea: Where did all the pellets go? Limnology and Oceanography 44: 1388-1399

Villafane V, Helbling EW, Holm-Hansen O (1993) Phytoplankton around Elephant Island, Antarctica. Polar Biology 13: 183-191

von Bodungen B (1986) Phytoplankton growth and krill grazing during spring in the Bransfield Strait, Antarctica - Implications from sediment trap collections. Polar Biology 6: 153-160

von Bodungen B, Fischer G, Nöthig E-M, Wefer G (1987) Sedimentation of krill faeces during spring development of phytoplankton in Bransfield Strait, Antarctica. Mitteilungen der Geologischen und Palaontologischen Institute University of Hamburg 62: 243-257

von Bodungen B, Smetacek VS, Tilzer MM, Zeitzschel B (1986) Primary production and sedimentation during spring in the Antarctic Peninsula region. Deep-Sea Research 33: 177-194

Voronina NM, Kolosova EG, Melnikov IA (2001) Zooplankton life under the perennial Antarctic Sea ice. Polar Biology 24: 401-407

Waite AM, Thompson PA, Harrison PJ (1992) Does energy control the sinking rates of marine diatoms? Limnology and Oceanography 37: 468-477

Wakeham SG, Hedges JI, Lee C, Pease TK (1993) Effects of poisons and preservatives on the composition of organic matter in a sediment trap experiment. Journal of Marine Research 51: 669-696

Walsh JJ, Dieterle DA, Lenes J (2001) A numerical analysis of carbon dynamics of the Southern Ocean phytoplankton community: the roles of light and grazing in effecting both sequestration of atmospheric CO_2 and food availability to larval krill. Deep-Sea Research I 48: 1-48

Wang Z (1995) Factors influencing seasonal changes in the respiration of *Drepanopus bispinosus* (Copepoda: Calanoida) in Burton Lake, a marine derived saline lake in the Vestfold Hills, Antarctica. Antarctic Record 39: 79-93

Ward P, Shreeve P (1999) The spring mesozooplankton community at South Georgia: a comparison of shelf and oceanic sites. Polar Biology 22: 289-301

Wassmann P (1998) Retention versus export food chains: processes controlling sinking loss from marine pelagic systems. Hydrobiologia 363: 29-57

Wassmann P, Hansen L, Andreassen IJ, Wexels Riser C, Urban-Rich J (1999) Distribution and sedimentation of faecal pellets on the Nordvestbanken shelf, northern Norway, in 1994. Sarsia 84: 239-252

Wassmann P, Martinez R, Vernet M (1994) Respiration and biochemical composition of sedimenting organic matter during summer in the Barents Sea. Continental Shelf Research 14: 79-90

Wassmann P, Peinert R, Smetacek V (1991) Patterns of production and sedimentation in the boreal and polar Northeast Atlantic. Polar Research 10: 209-228

Watanabe K, Satoh H, Hoshiai T (1990) Seasonal variation in ice algal assemblages in the fast ice near Syowa station in 1983/84. In KR Kerry, G Hempel (eds) Antarctic Ecosystems: ecological change and conservation. Springer-Verlag Berlin, Heidelberg, p 136-142

Waters RL, van den Enden R, Marchant HJ (2000) Summer microbial ecology off East Antarctica (80-150°E): protistan community structure and bacterial abundance. Deep-Sea Research II 47: 2401-2435

Wefer G (1989) Particle flux in the ocean: effects of episodic production. In WH Berger, VS Smetacek, G Wefer (eds) Productivity of the ocean: present and past. John Wiley Sons Ltd., Chichester, p 139-153

Wefer G, Fischer G (1991) Annual primary production and export flux in the Southern Ocean from sediment trap data. Marine Chemistry 35: 597-613

Wefer G, Fischer G, Fuetterer D, Gersonde R (1988) Seasonal particle flux in the Bransfield Strait, Antarctica. Deep-Sea Research 35: 891-898

Wickham SA (1995) Trophic relations between cyclopoid copepods and ciliated protists: Complex interactions link the microbial and classical food webs. Limnology and Oceanography: 1173-1181

Williams PJl, von Bodungen B, Bathmann U, Berger WH, Eppley RW, Feldman GC, Fischer G, Legendre L, Minster J-F, Reynolds CS, Smetacek VS, Toggweiler JR (1989) Group report: export productivity from the photic zone. In WH Berger, VS Smetacek, G Wefer (eds) Productivity of the ocean: present and past. John Wiley Sons Ltd., Chichester, p 99-115

Williams R, Conway DVP, Hunt HG (1994) The role of copepods in the planktonic ecosystems of mixed and stratified waters of the European shelf seas. Hydrobiologia 292/293: 521-530

Working Group 2 (1988) Preservation of organic matter in sediment traps. In P Wassmann, A-S Heiskanen (eds) Sediment trap studies in the Nordic countries 1, Tvarminne Zoological Station, Hanko, Finland, 24-28 February, 1988. p 188-192

Yakovlev SN (1984) Reproductive cycle of Antarctic sea urchin *Sterechinus neumayerii* in Davis Sea. Biologiya Morya (English Translation) 5: 35-39

Zar JH (1984) Biostatistical analysis. Prentice-Hall International, Inc., New Jersey, 123 pp

Appendix 1

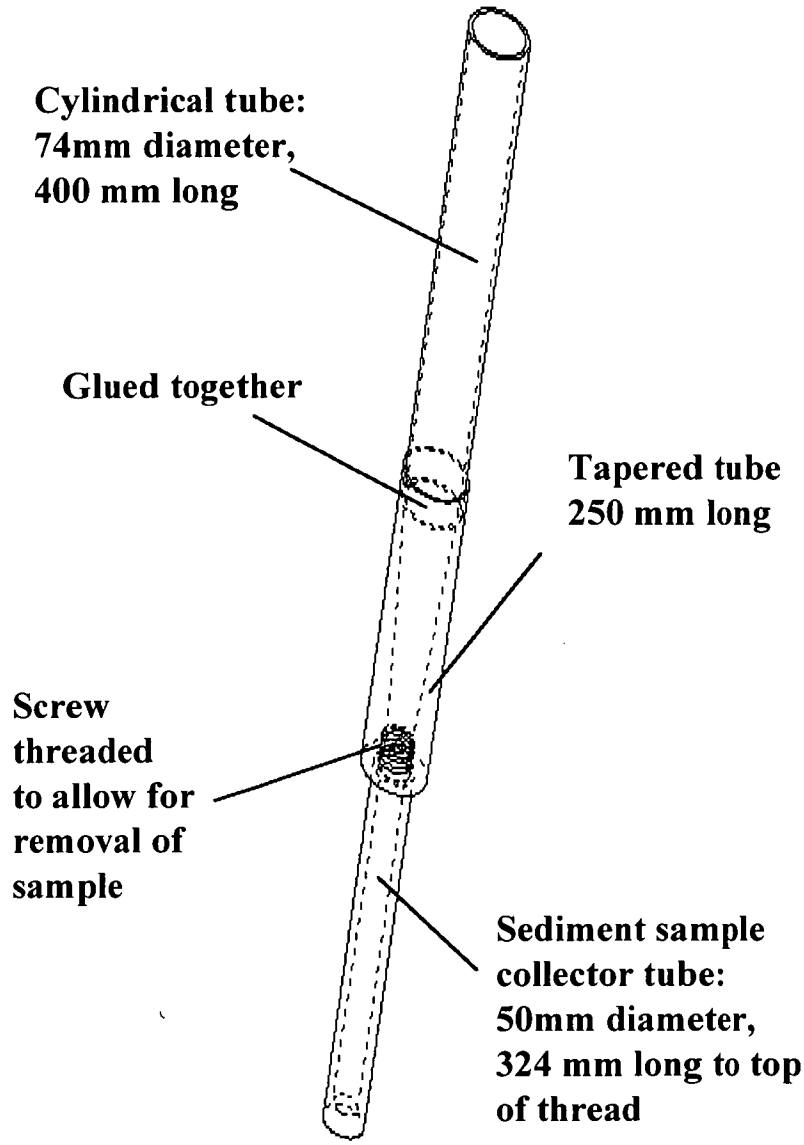


Figure A1.1. Sediment trap design. Traps were made of poly-vinyl chloride. Overall length of unit = 925 mm, largest diameter of unit = 74 mm.

Appendix 2

Table A2.1. Percentage of cells that were intact, vesicularised, or burst immediately after treatment and after one week. L1 & L2 represent the upper and lower 95% confidence limits. MCBR = Mercuric chloride & brine, MC = Mercuric chloride, GLBR = Glutaraldehyde & brine, GL = Glutaraldehyde.

		% Intact			Vesic			Burst		
		Mean	L1	L2	Mean	L1	L2	Mean	L1	L2
Polarella sp.										
Initial	MCBR	58	64	52	41	46	35	1	2	0
	MC	69	73	65	28	32	25	2	4	0
	GLBR	81	83	79	18	21	16	0	1	0
	GL	81	83	78	18	20	15	1	2	0
1 week	MCBR	71	82	59	28	40	18	0	0	0
	MC	75	84	66	24	33	16	0	0	0
	GLBR	84	95	68	16	32	5	0	0	0
	GL	84	92	74	14	24	6	1	5	0
Pyramimonas sp.										
Initial	MCBR	15	19	11	85	88	81	0	0	0
	MC	9	12	6	90	92	87	1	1	0
	GLBR	70	75	64	30	36	25	0	0	0
	GL	73	77	68	27	32	23	0	0	0
1 week	MCBR	14	21	8	86	92	79	0	0	0
	MC	12	19	7	88	93	81	0	0	0
	GLBR	91	96	85	9	15	4	0	0	0
	GL	91	92	90	9	10	8	0	0	0
HDIN										
Initial	MCBR	0	0	0	99	100	98	1	2	0
	MC	0	0	0	97	99	93	3	7	1
	GLBR	99	100	97	1	3	0	0	0	0
	GL	100	100	99	0	1	0	0	0	0
1 week	MCBR	0	0	0	98	99	86	2	14	1
	MC	0	0	0	100	99	95	0	0	0
	GLBR	99	99	92	1	8	1	0	0	0
	GL	99	99	92	1	8	1	0	0	0
Hflagellate										
Initial	MCBR	3	8	0	91	96	85	3	5	1
	MC	2	5	0	95	98	91	1	3	0
	GLBR	78	85	70	21	29	14	0	0	0
	GL	89	97	79	11	21	3	0	0	0
1 week	MCBR	12	33	1	80	94	59	4	20	0
	MC	0	2	1	98	99	88	1	9	1
	GLBR	66	71	61	32	39	26	0	0	0
	GL	75	85	64	23	32	15	0	0	0
Fragillariopsis sp.										
Initial	MCBR	17	31	7	83	93	69	0	0	0
	MC	7	17	1	93	99	83	0	0	0
	GLBR	60	71	50	40	50	29	0	0	0
	GL	59	71	46	41	54	29	0	0	0
1 week	MCBR	16	29	7	84	93	71	0	0	0
	MC	3	17	1	97	99	83	0	0	0
	GLBR	49	61	37	51	63	39	0	0	0
	GL	60	76	43	40	57	24	0	0	0

Appendix 3

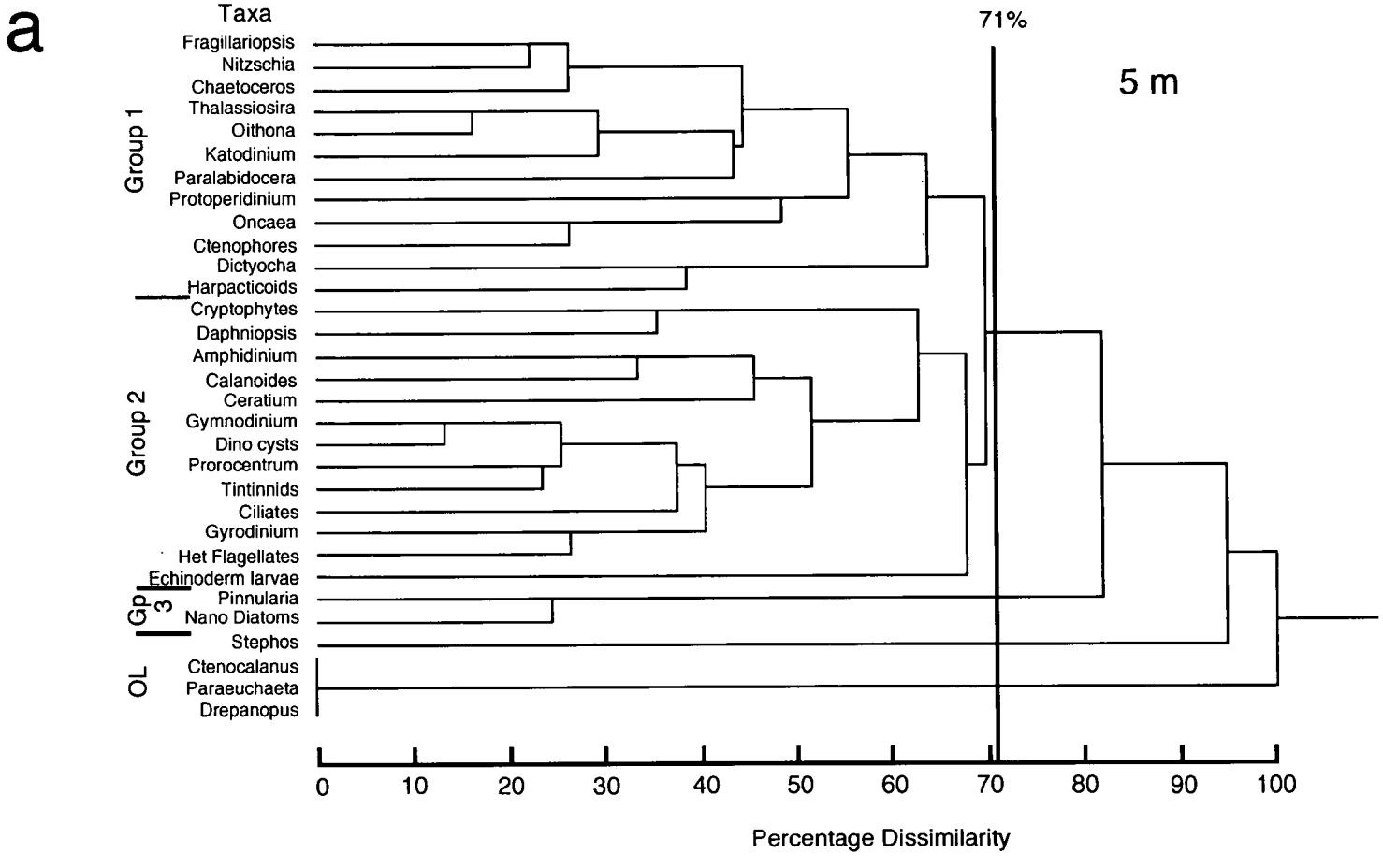


Figure A3.1a. Multivariate analysis of species associations at 5 m depth shows the dendrogram of cluster analysis based on the Bray-Curtis dissimilarity index with UPGMA linkage. Only the genera are listed, for species information refer to the text. GP = Group, OL = Outlier.

b

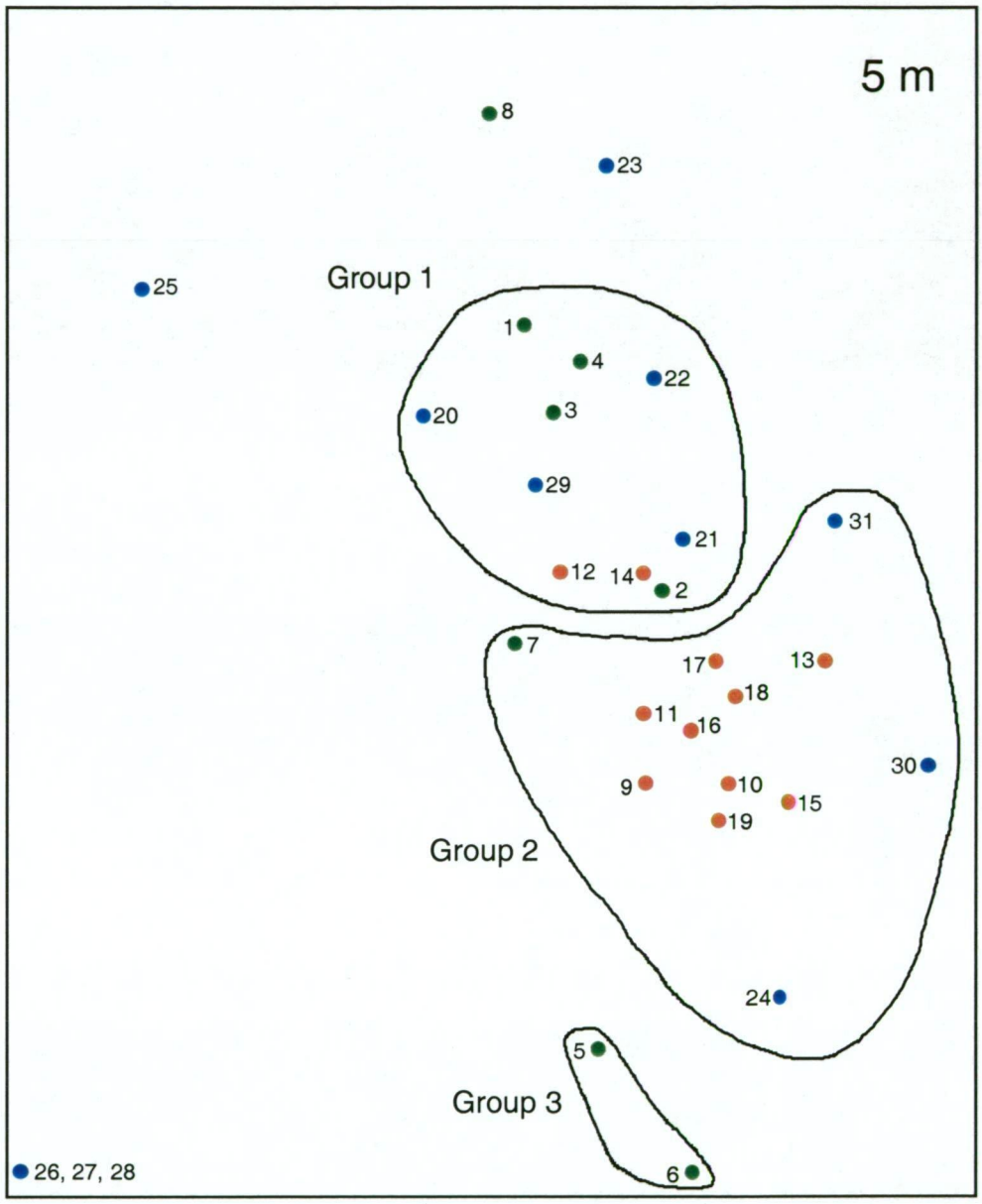


Figure A3.1.b Multivariate analysis of species associations at 5 m depth. shows the ordination plot of the cluster analysis using NMDS. Colours denote taxa; green = phytoplankton, red = protozoa, blue = metazoa. Numbers denote species as per the text. Axis scales are not shown as they are relative in NMDS.

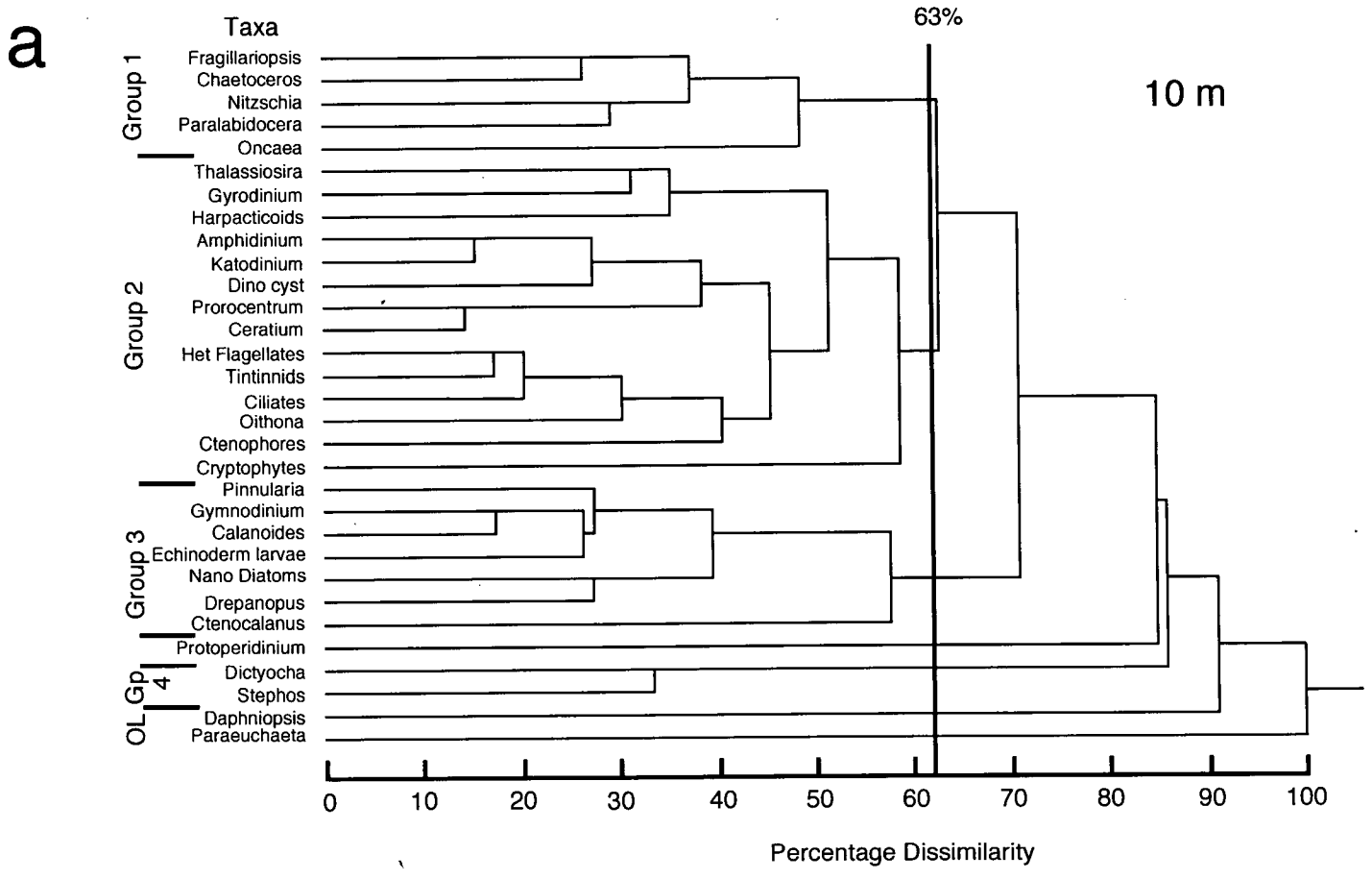


Figure A3.2a. Multivariate analysis of species associations at 10 m depth shows the dendrogram of cluster analysis based on the Bray-Curtis dissimilarity index with UPGMA linkage. Only the genera are listed, for species information refer to the text. GP = Group, OL = Outlier.

b

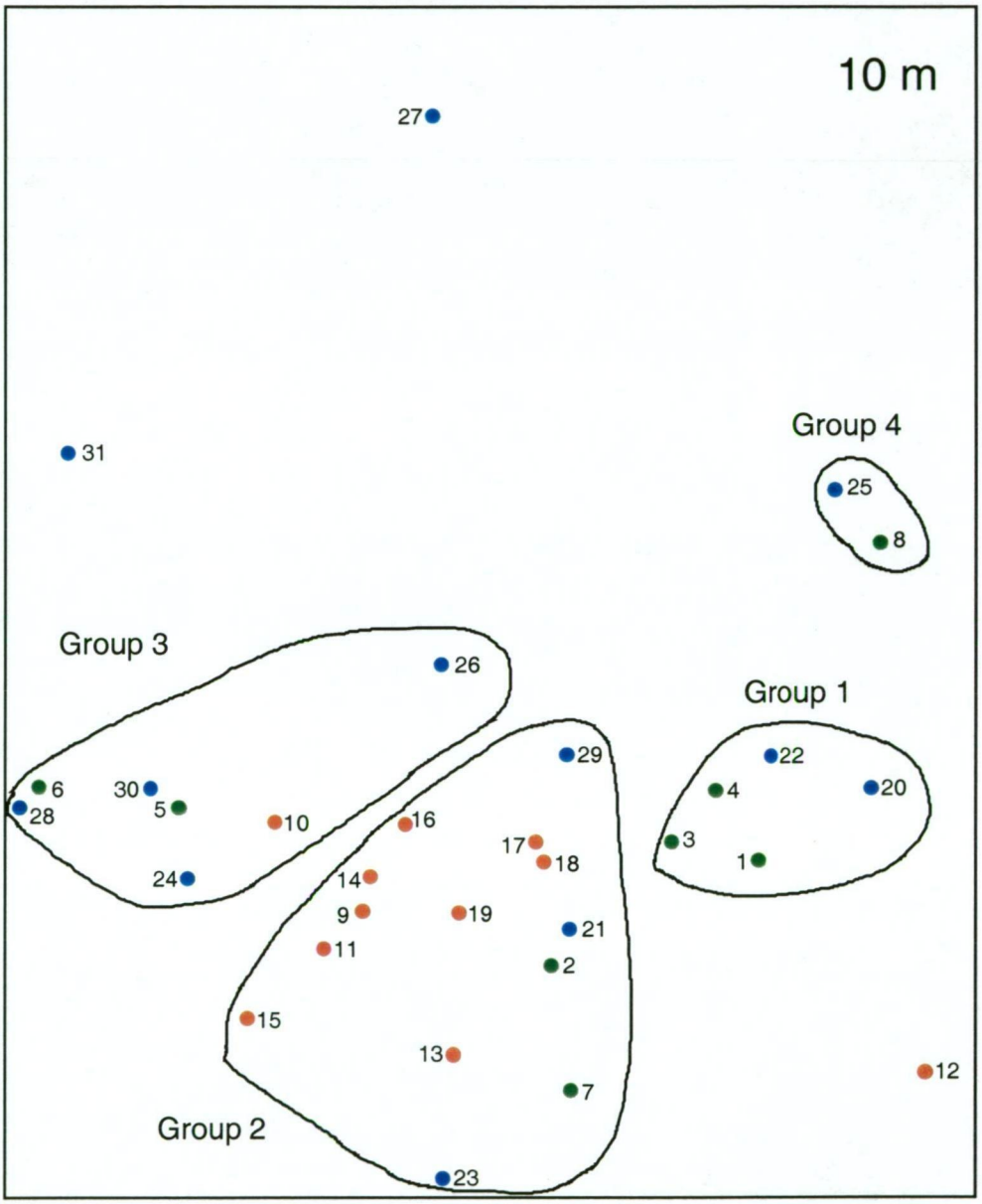


Figure A3.2b. Multivariate analysis of species associations at 10 m depth shows the ordination plot of the cluster analysis using NMDS. Colours denote taxa; green = phytoplankton, red = protozoa, blue = metazoa. Numbers denote species as per the text. Axis scales are not shown as they are relative in NMDS.

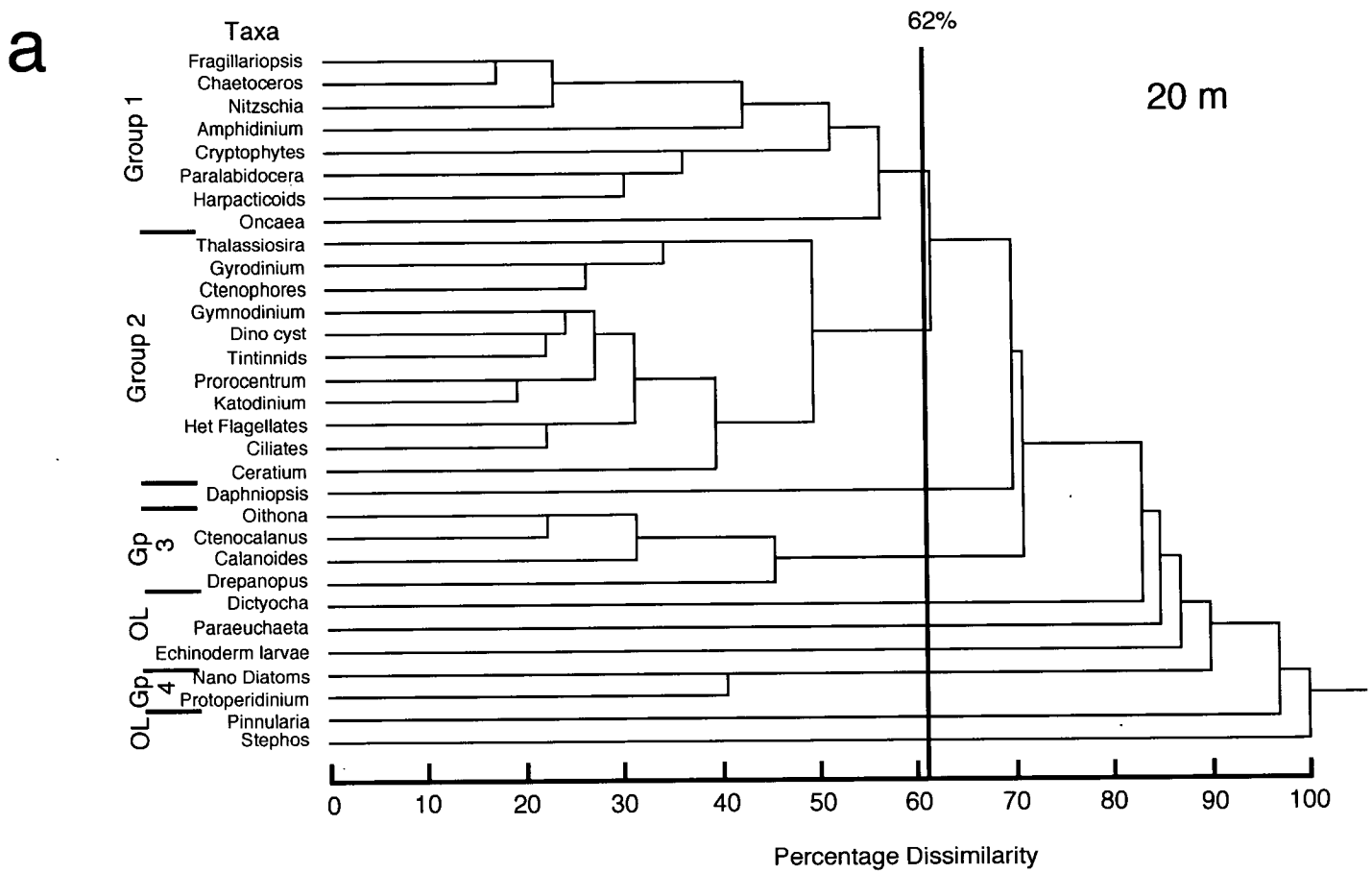


Figure A3.3a. Multivariate analysis of species associations at 20 m depth shows the dendrogram of cluster analysis based on the Bray-Curtis dissimilarity index with UPGMA linkage. Only the genera are listed, for species information refer to the text. GP = Group, OL = Outlier.

b

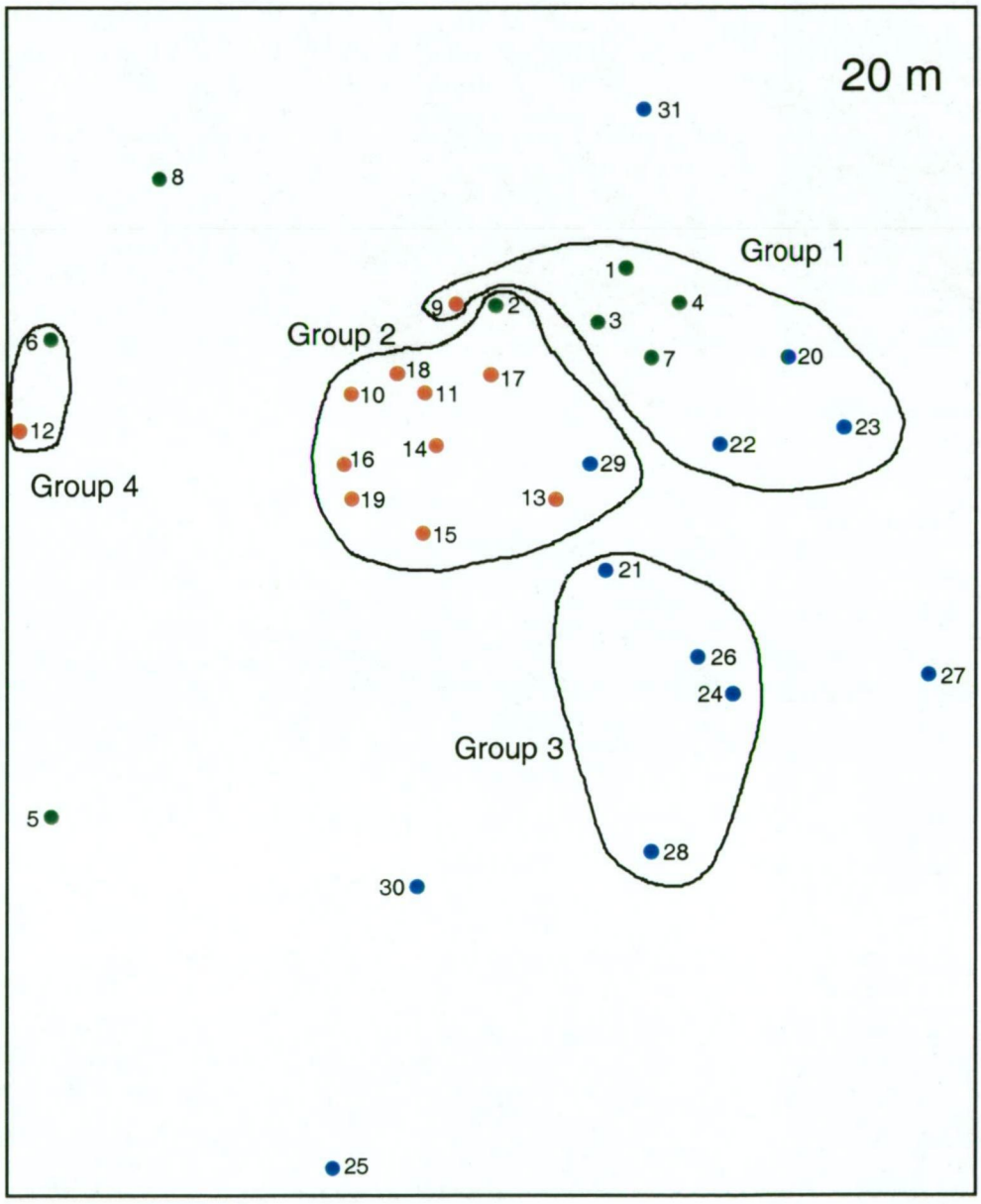


Figure A3.3b. Multivariate analysis of species associations at 20 m depth shows the ordination plot of the cluster analysis using NMDS. Colours denote taxa; green = phytoplankton, red = protozoa, blue = metazoa. Numbers denote species as per the text. Axis scales are not shown as they are relative in NMDS.

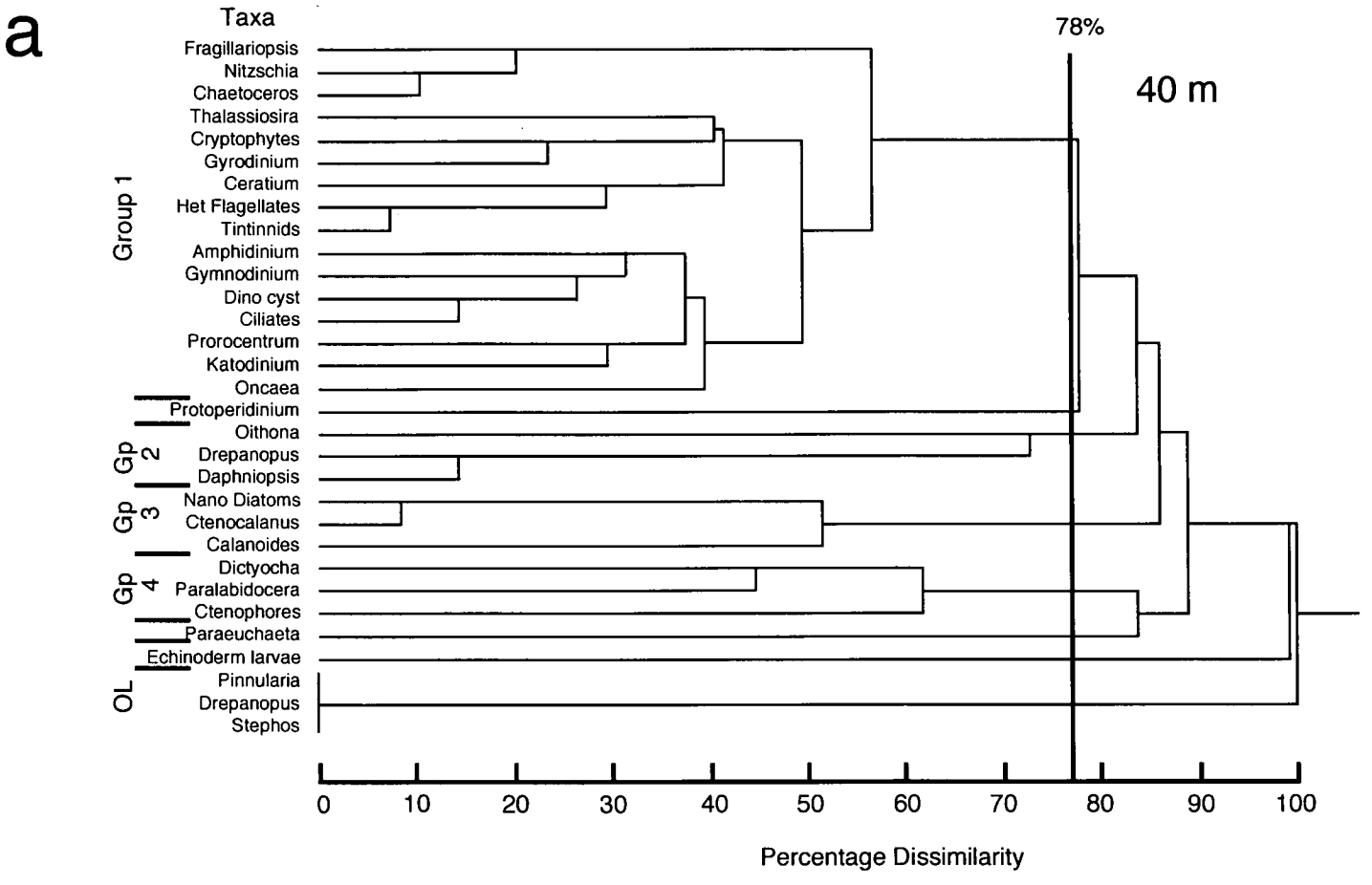


Figure A3.4a. Multivariate analysis of species associations at 40 m depth. shows the dendrogram of cluster analysis based on the Bray-Curtis dissimilarity index with UPGMA linkage. Only the genera are listed, for species information refer to the text. GP = Group, OL = Outlier.

b

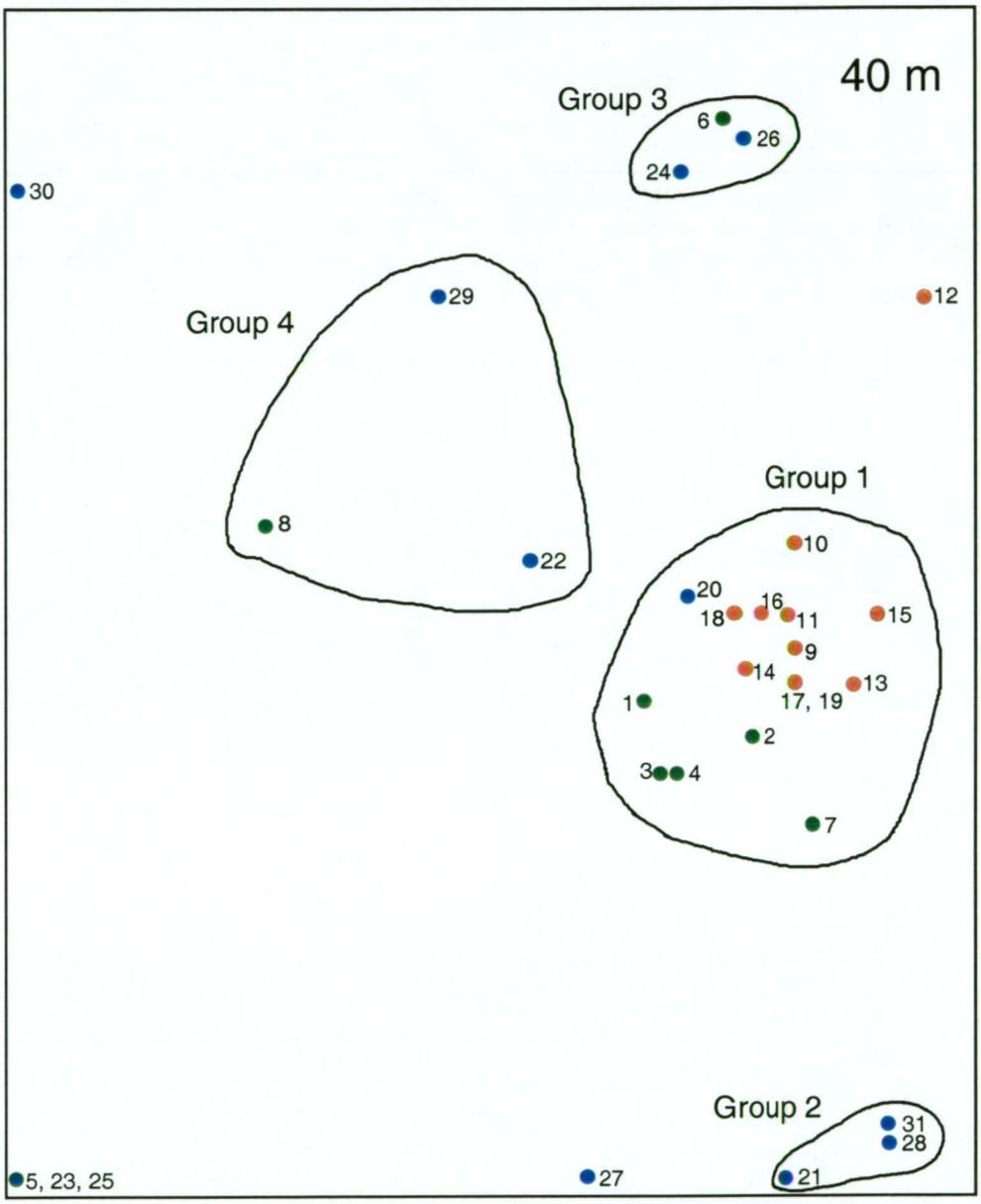


Figure A3.4b. Multivariate analysis of species associations at 40 m depth shows the ordination plot of the cluster analysis using NMDS. Colours denote taxa; green = phytoplankton, red = protozoa, blue = metazoa. Numbers denote species as per the text. Axis scales are not shown as they are relative in NMDS.

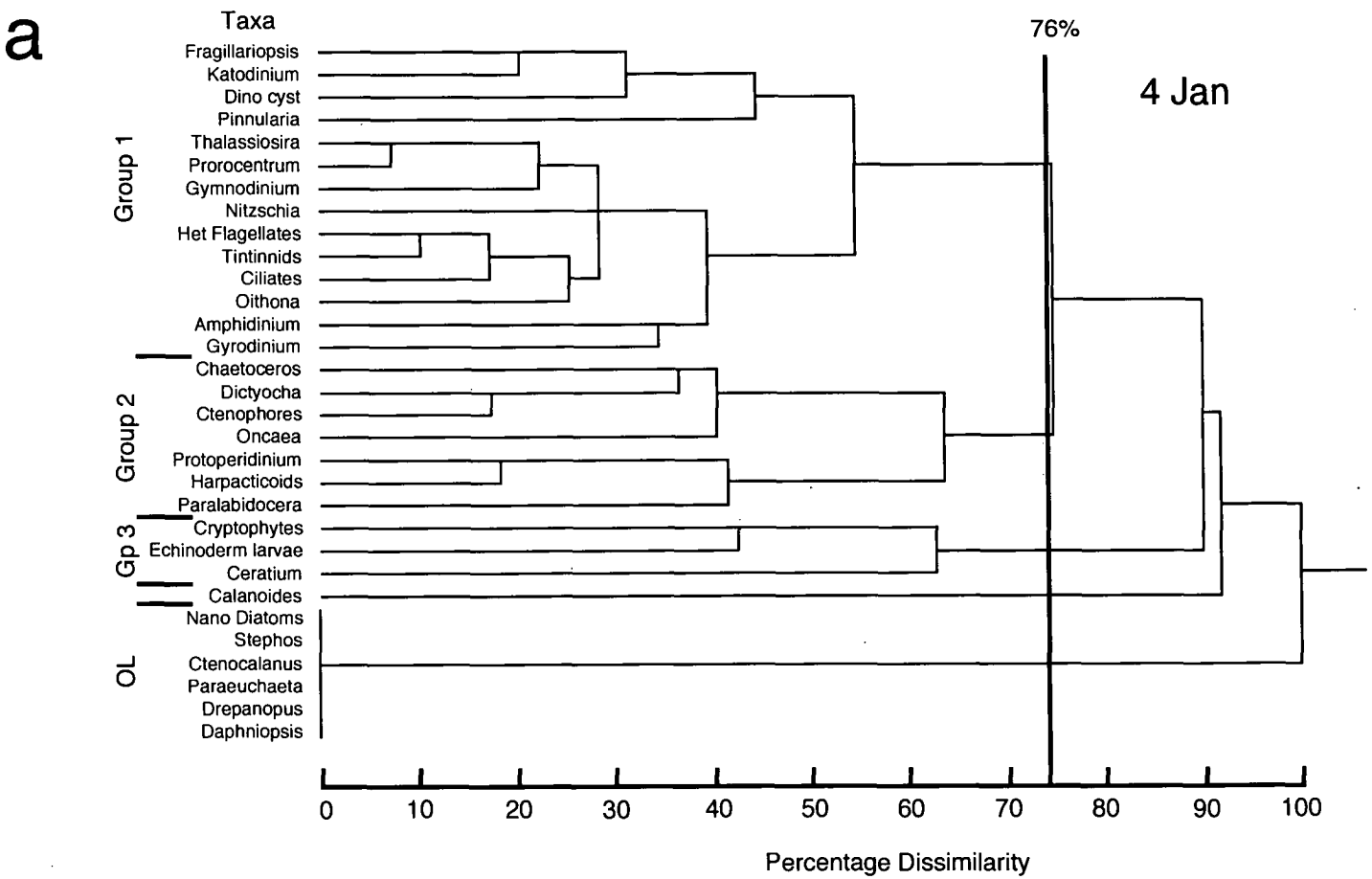


Figure A3.5a. Multivariate analysis of species associations at all depths on 4 January shows the dendrogram of cluster analysis based on the Bray-Curtis dissimilarity index with UPGMA linkage. Only the genera are listed, for species information refer to the text. GP = Group, OL = Outlier.

b

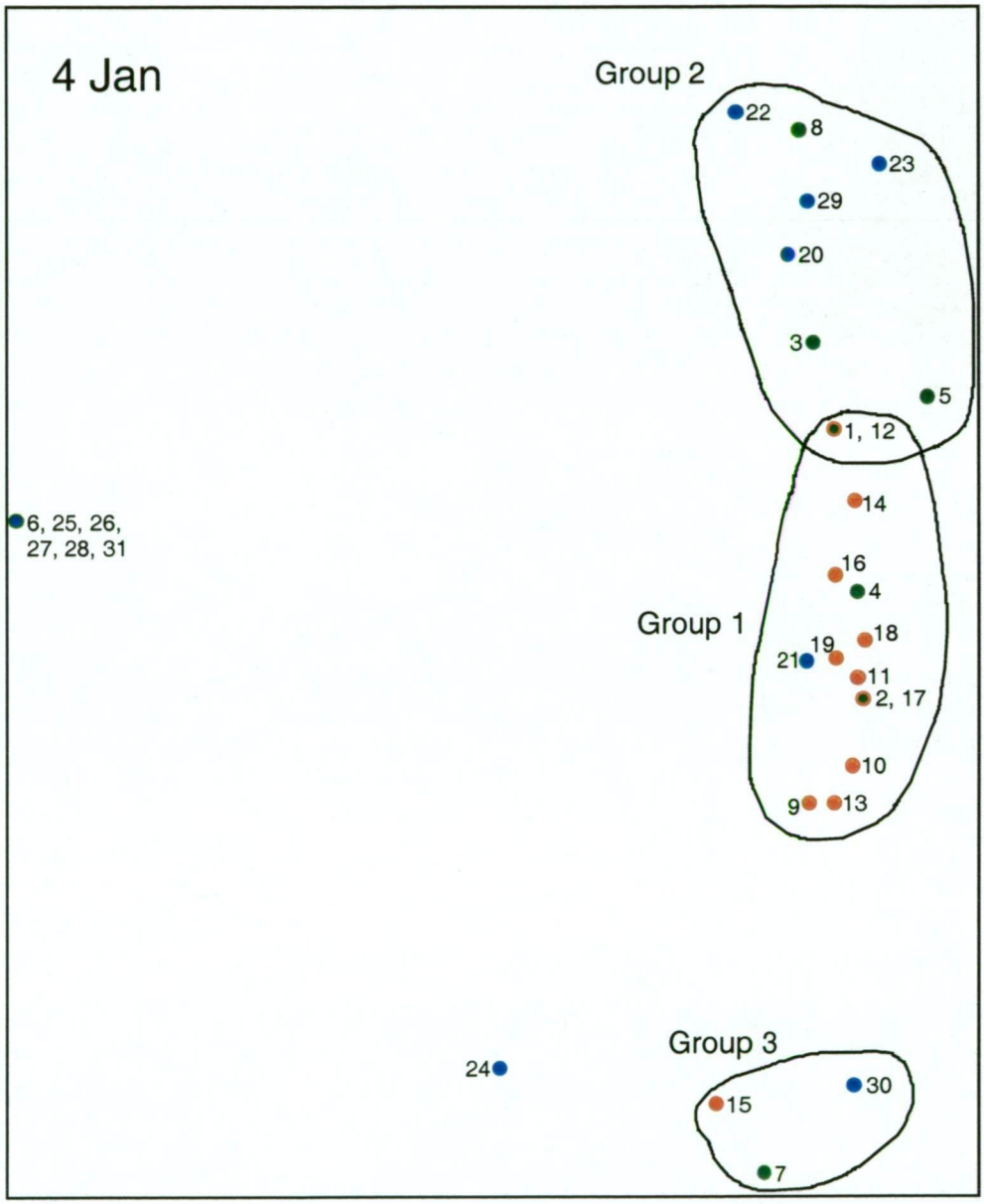


Figure A3.5b. Multivariate analysis of species associations at all depths on 4 January shows the ordination plot of the cluster analysis using NMDS. Colours denote taxa; green = phytoplankton, red = protozoa, blue = metazoa. Numbers denote species as per the text. Axis scales are not shown as they are relative in NMDS.

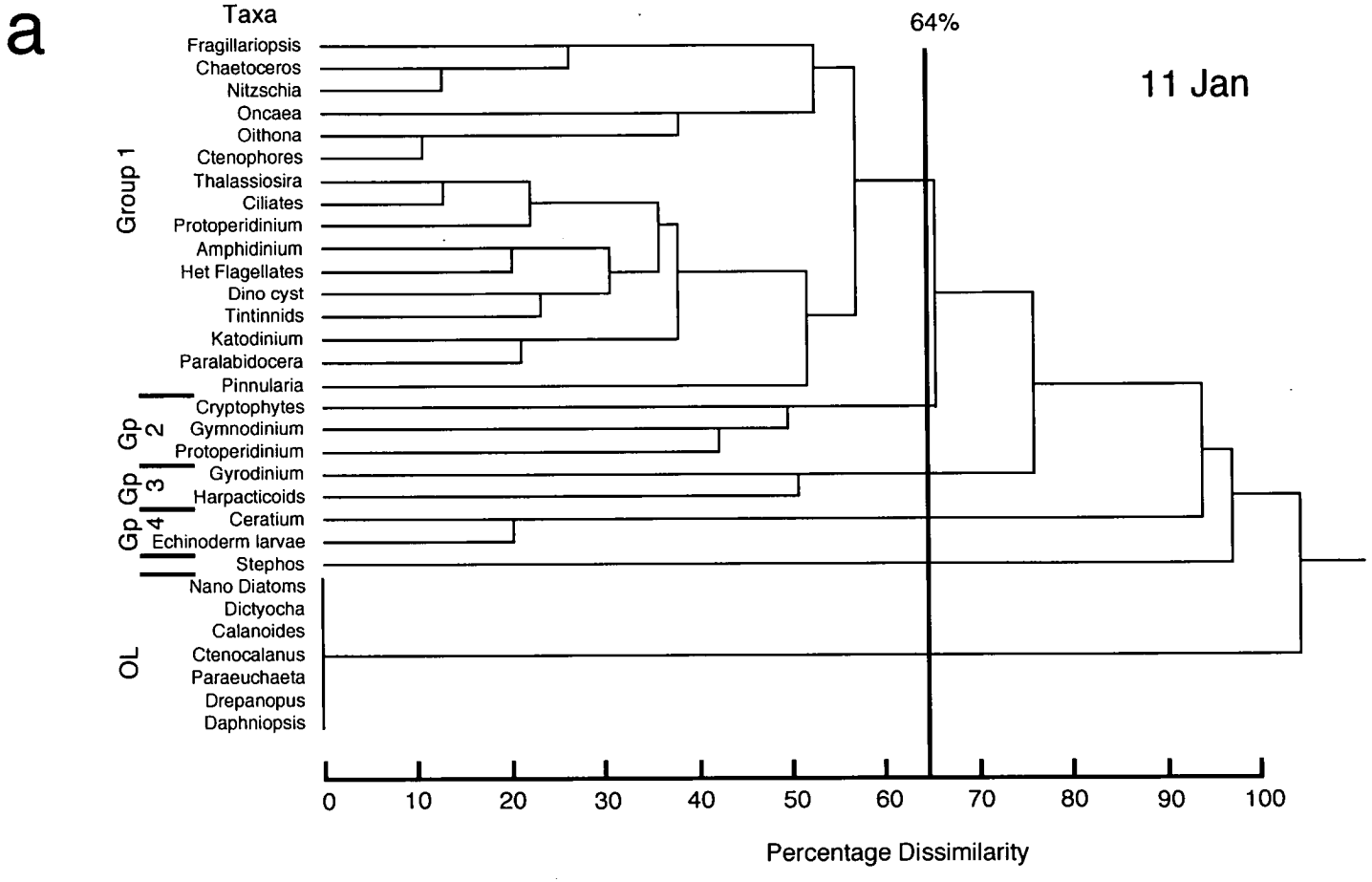


Figure A3.6a. Multivariate analysis of species associations at all depths on 11 January shows the dendrogram of cluster analysis based on the Bray-Curtis dissimilarity index with UPGMA linkage. Only the genera are listed, for species information refer to the text. GP = Group, OL = Outlier.

b

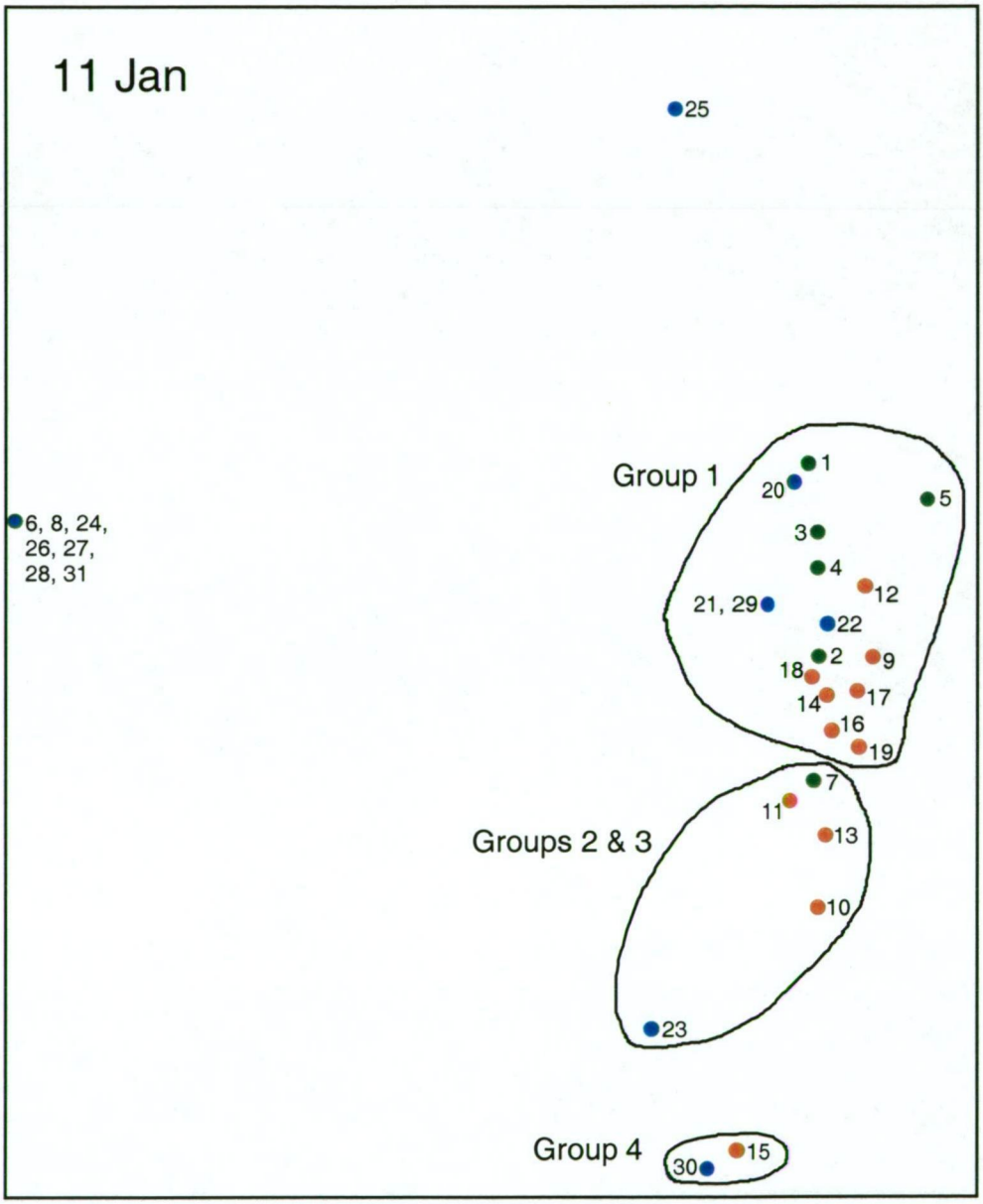


Figure A3.6b. Multivariate analysis of species associations at all depths on 11 January shows the ordination plot of the cluster analysis using NMDS. Colours denote taxa; green = phytoplankton, red = protozoa, blue = metazoa. Numbers denote species as per the text. Axis scales are not shown as they are relative in NMDS.

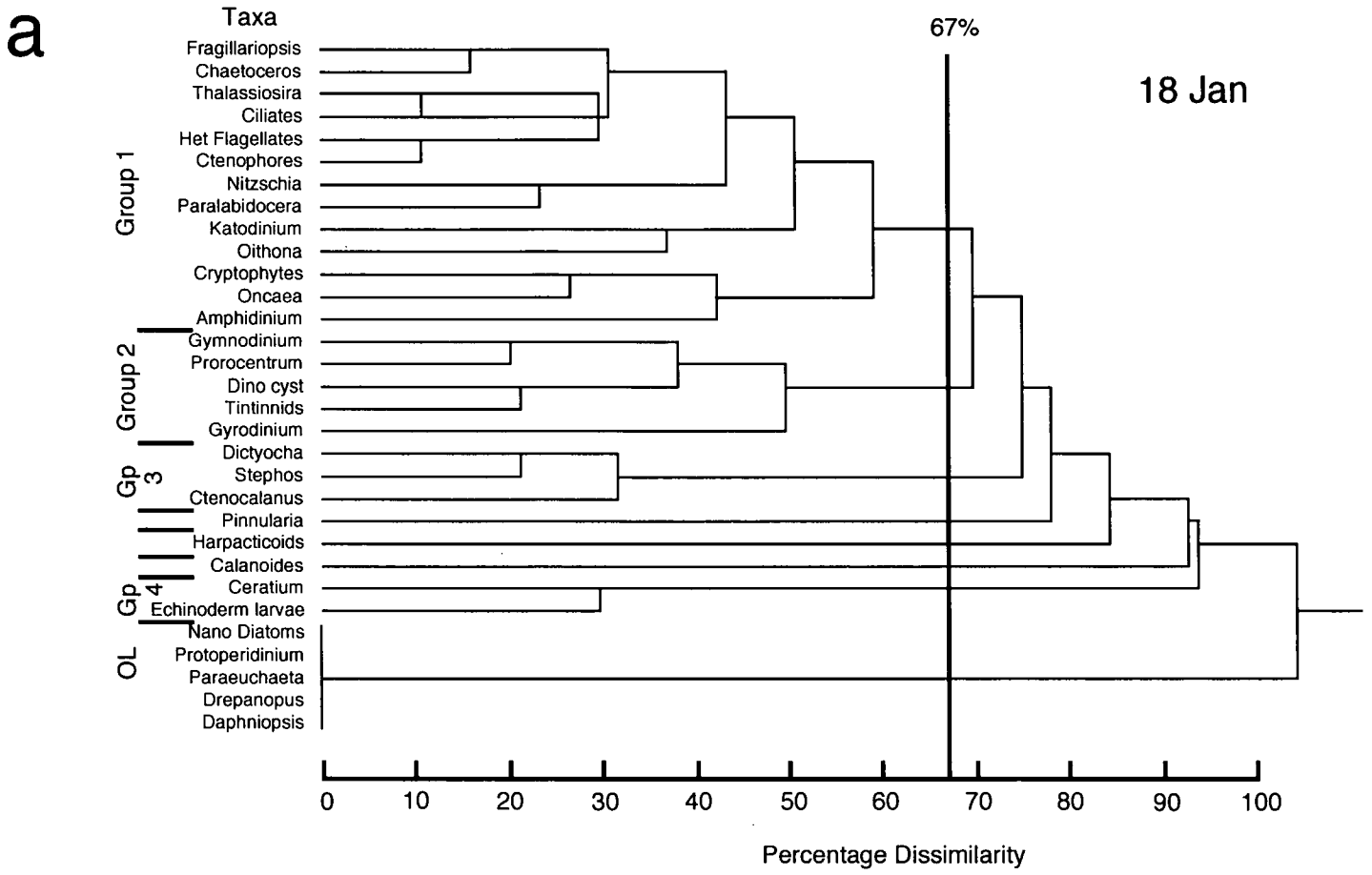


Figure A3.7. Multivariate analysis of species associations at all depths on 18 January shows the dendrogram of cluster analysis based on the Bray-Curtis dissimilarity index with UPGMA linkage. Only the genera are listed, for species information refer to the text. GP = Group, OL = Outlier.

b

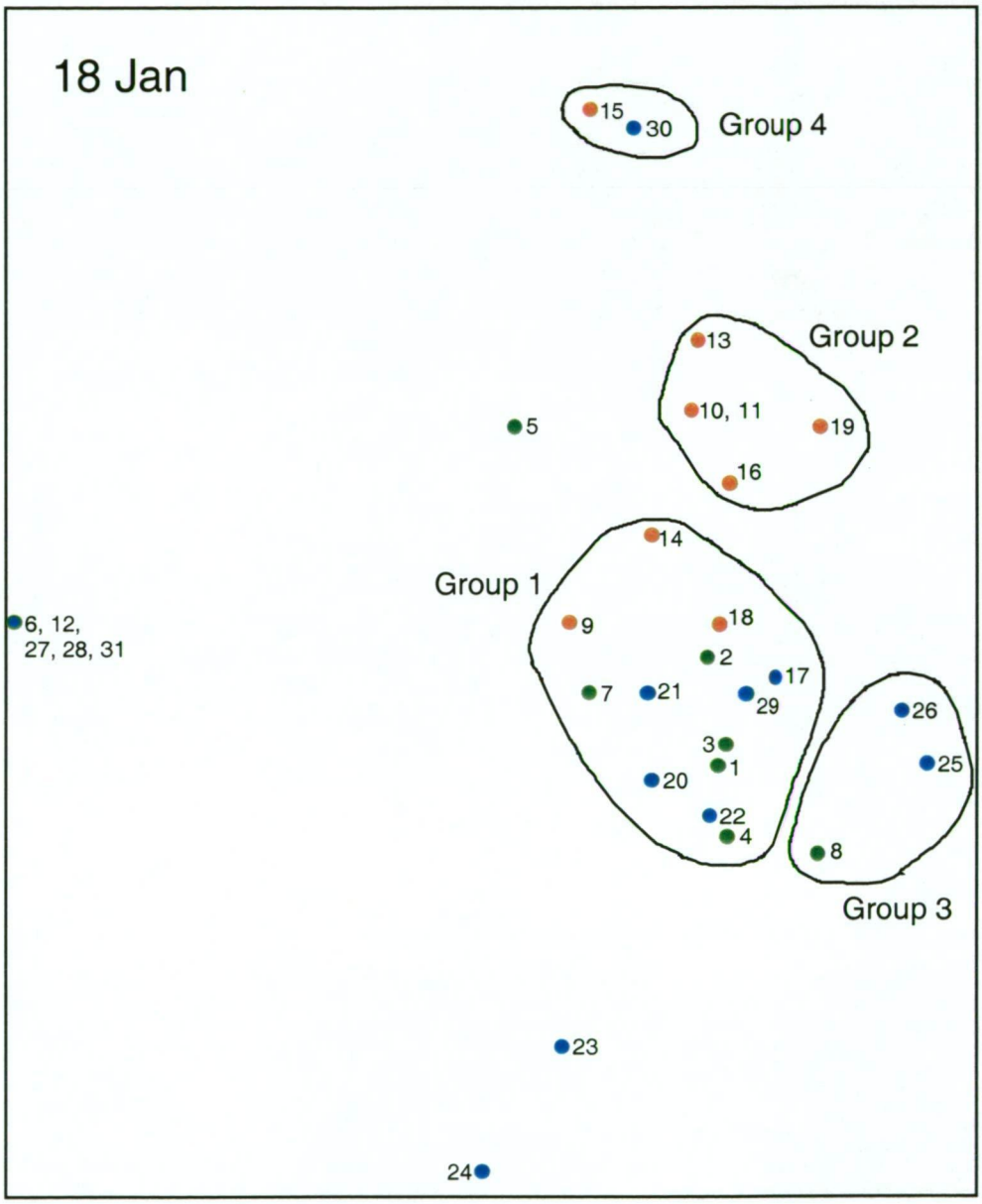


Figure A3.7b. Multivariate analysis of species associations at all depths on 18 January shows the ordination plot of the cluster analysis using NMDS. Colours denote taxa; green = phytoplankton, red = protozoa, blue = metazoa. Numbers denote species as per the text. Axis scales are not shown as they are relative in NMDS.

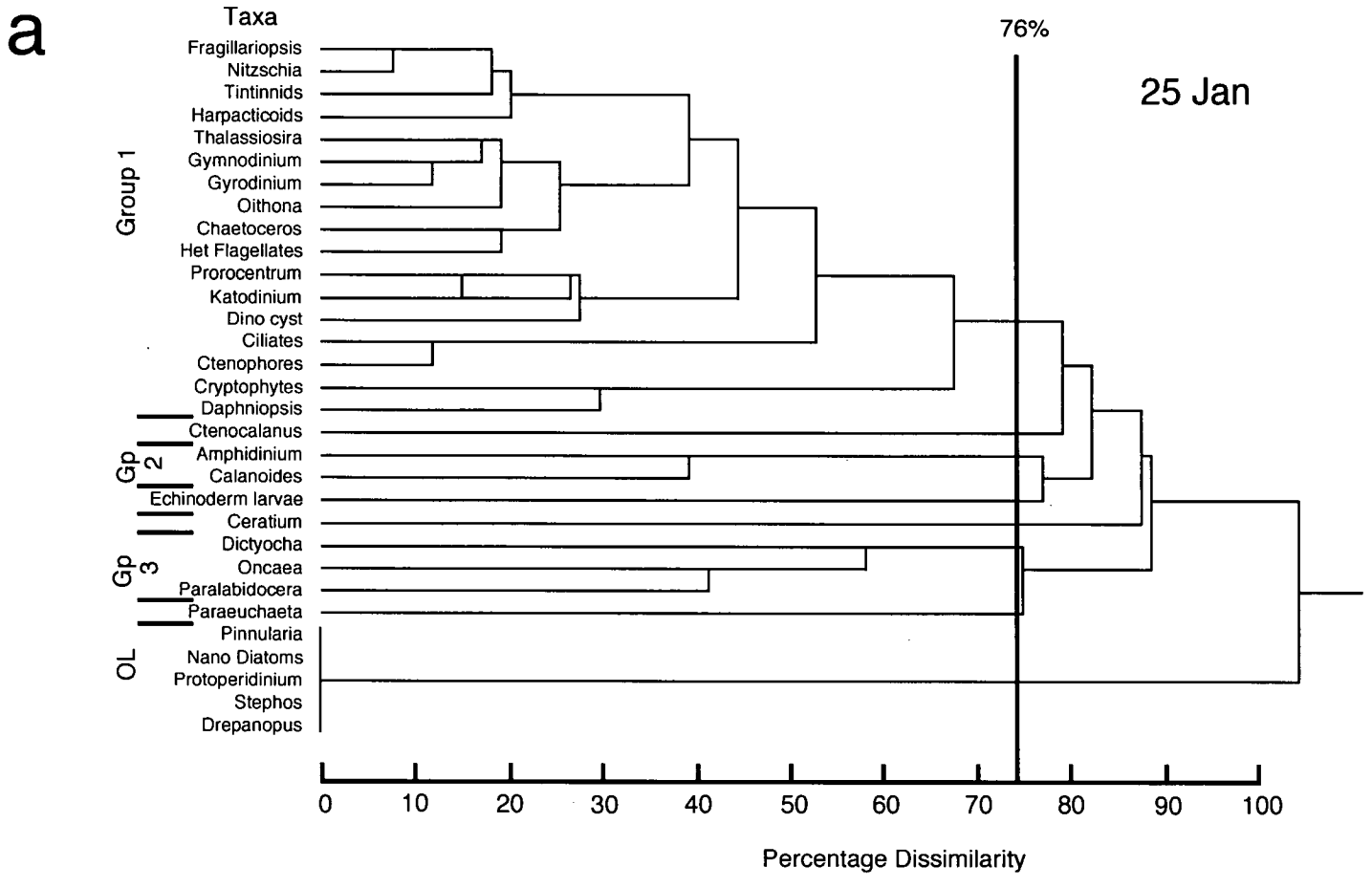


Figure A3.8a. Multivariate analysis of species associations at all depths on 25 January shows the dendrogram of cluster analysis based on the Bray-Curtis dissimilarity index with UPGMA linkage. Only the genera are listed, for species information refer to the text. GP = Group, OL = Outlier.

b

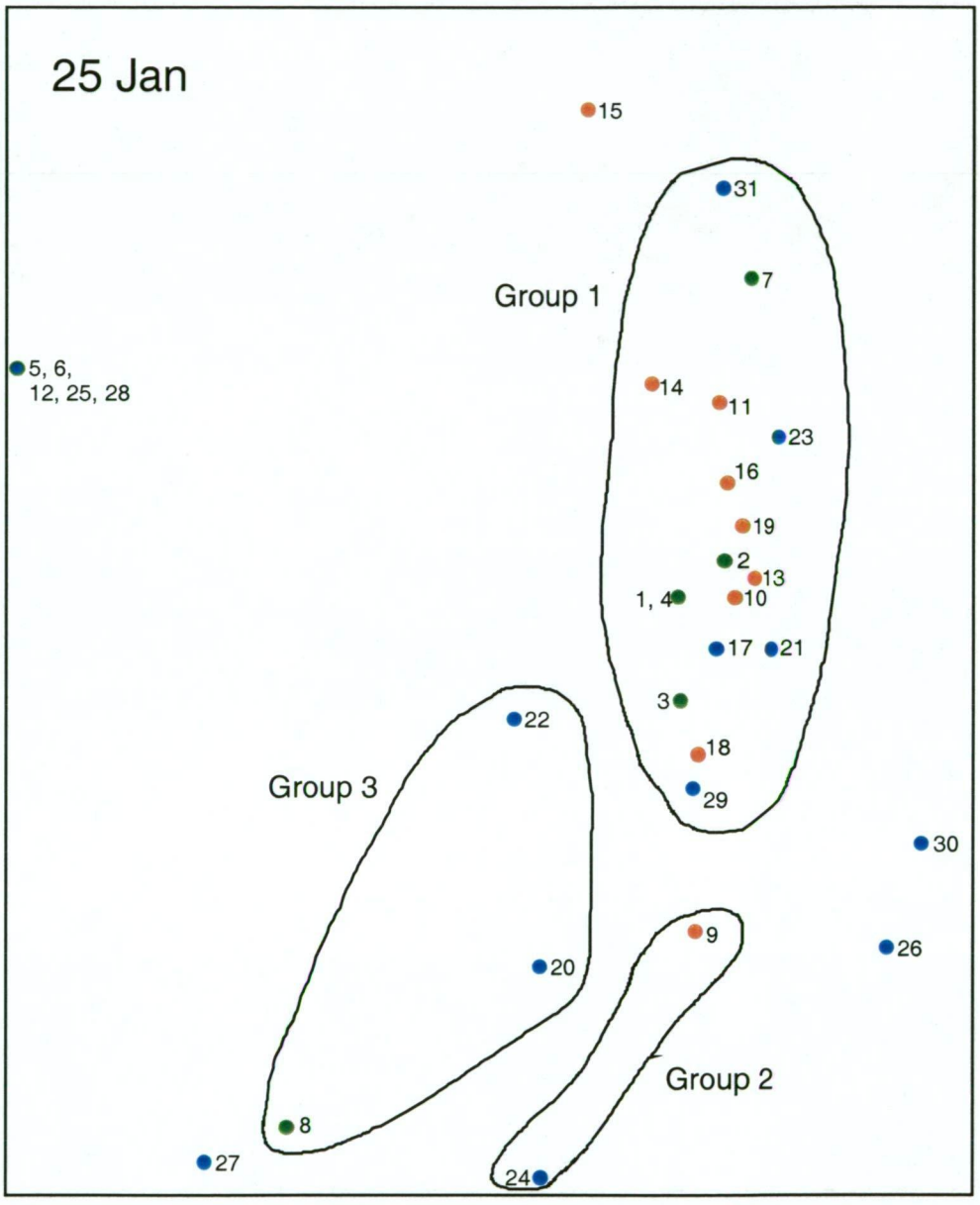


Figure A3.8b. Multivariate analysis of species associations at all depths on 25 January shows the ordination plot of the cluster analysis using NMDS. Colours denote taxa; green = phytoplankton, red = protozoa, blue = metazoa. Numbers denote species as per the text. Axis scales are not shown as they are relative in NMDS.

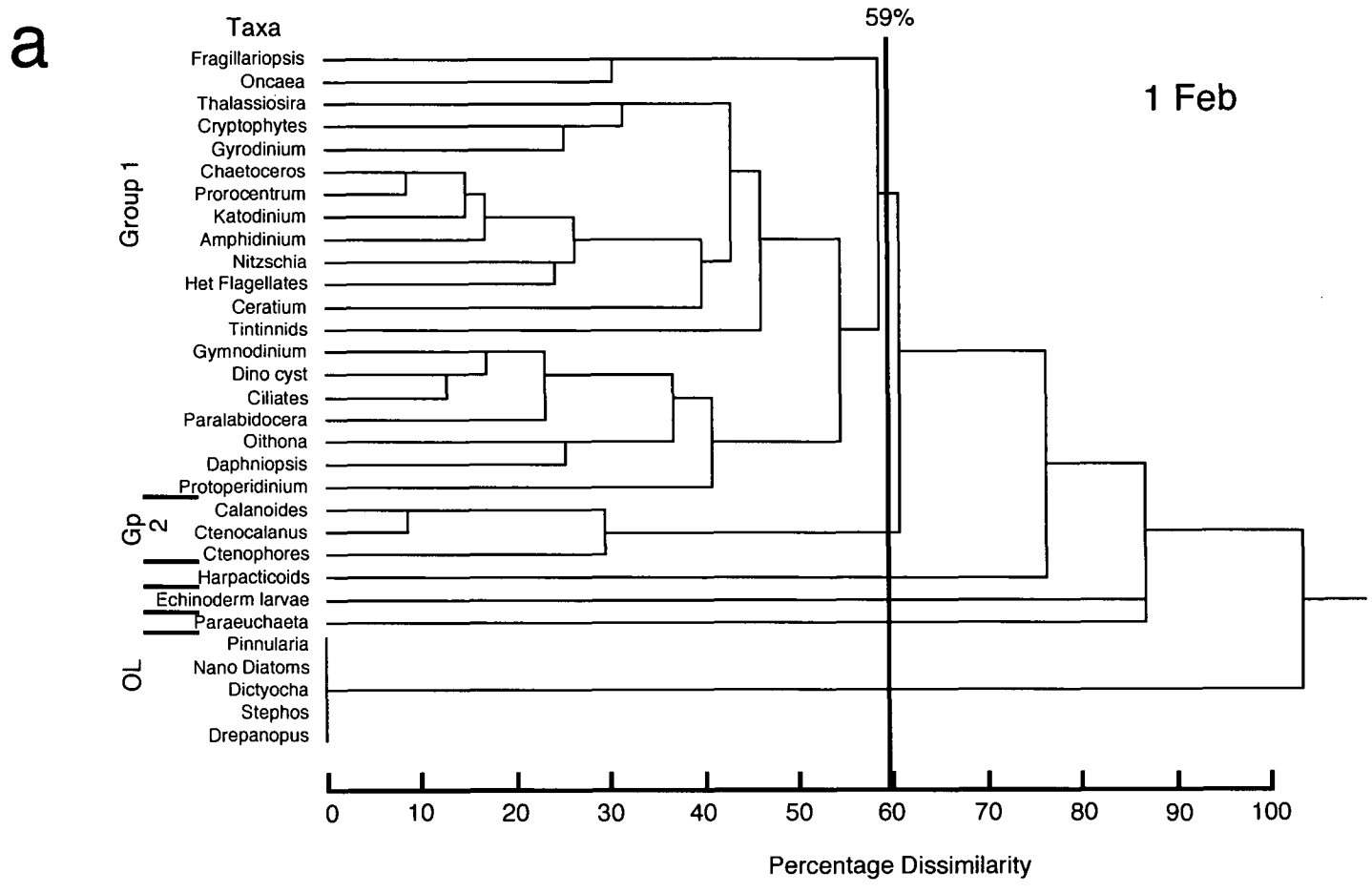


Figure A3.9a. Multivariate analysis of species associations at all depths on 1 February shows the dendrogram of cluster analysis based on the Bray-Curtis dissimilarity index with UPGMA linkage. Only the genera are listed, for species information refer to the text. GP = Group, OL = Outlier.

b

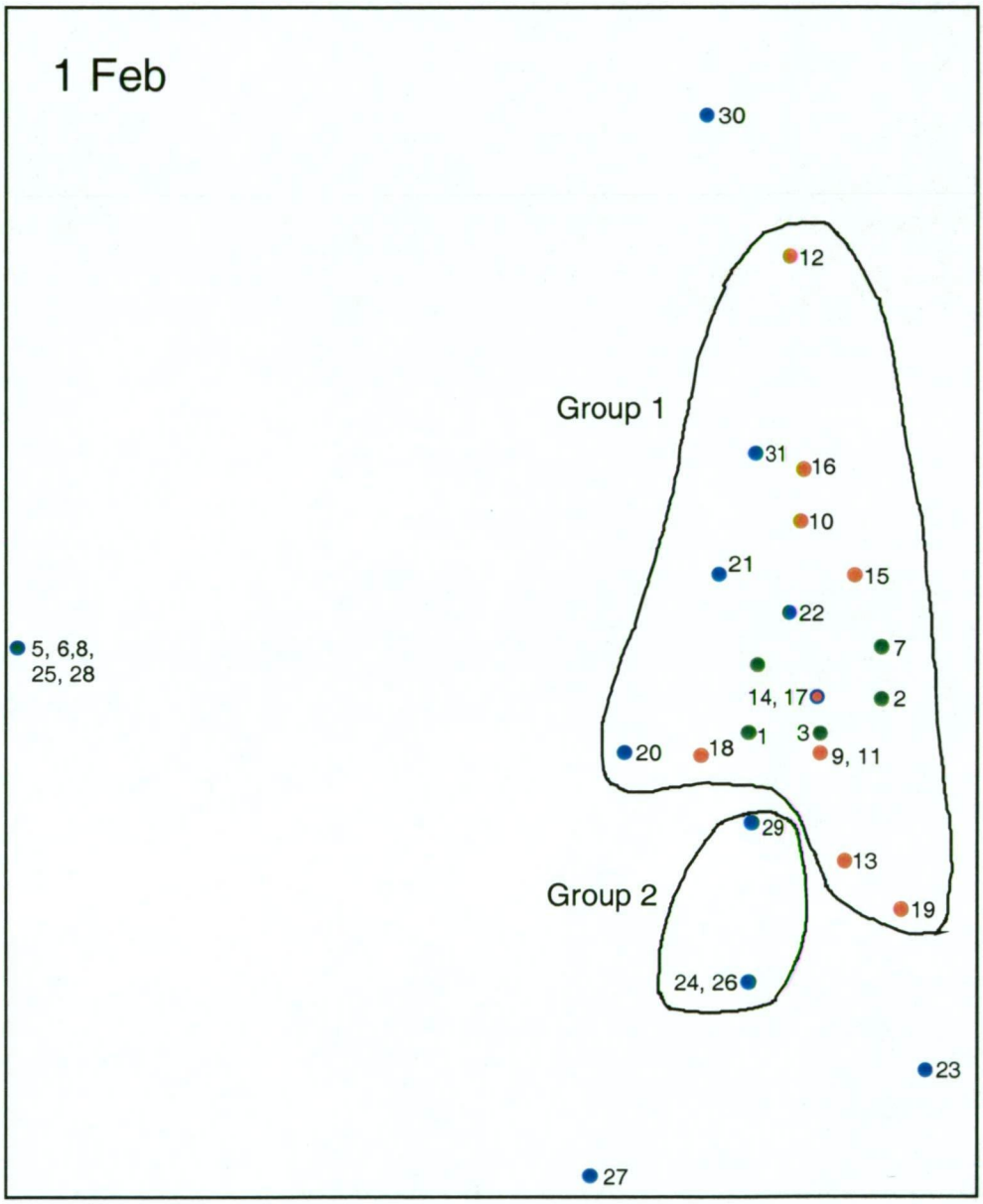


Figure A3.9b. Multivariate analysis of species associations at all depths on 1 February shows the ordination plot of the cluster analysis using NMDS. Colours denote taxa; green = phytoplankton, red = protozoa, blue = metazoa. Numbers denote species as per the text. Axis scales are not shown as they are relative in NMDS.

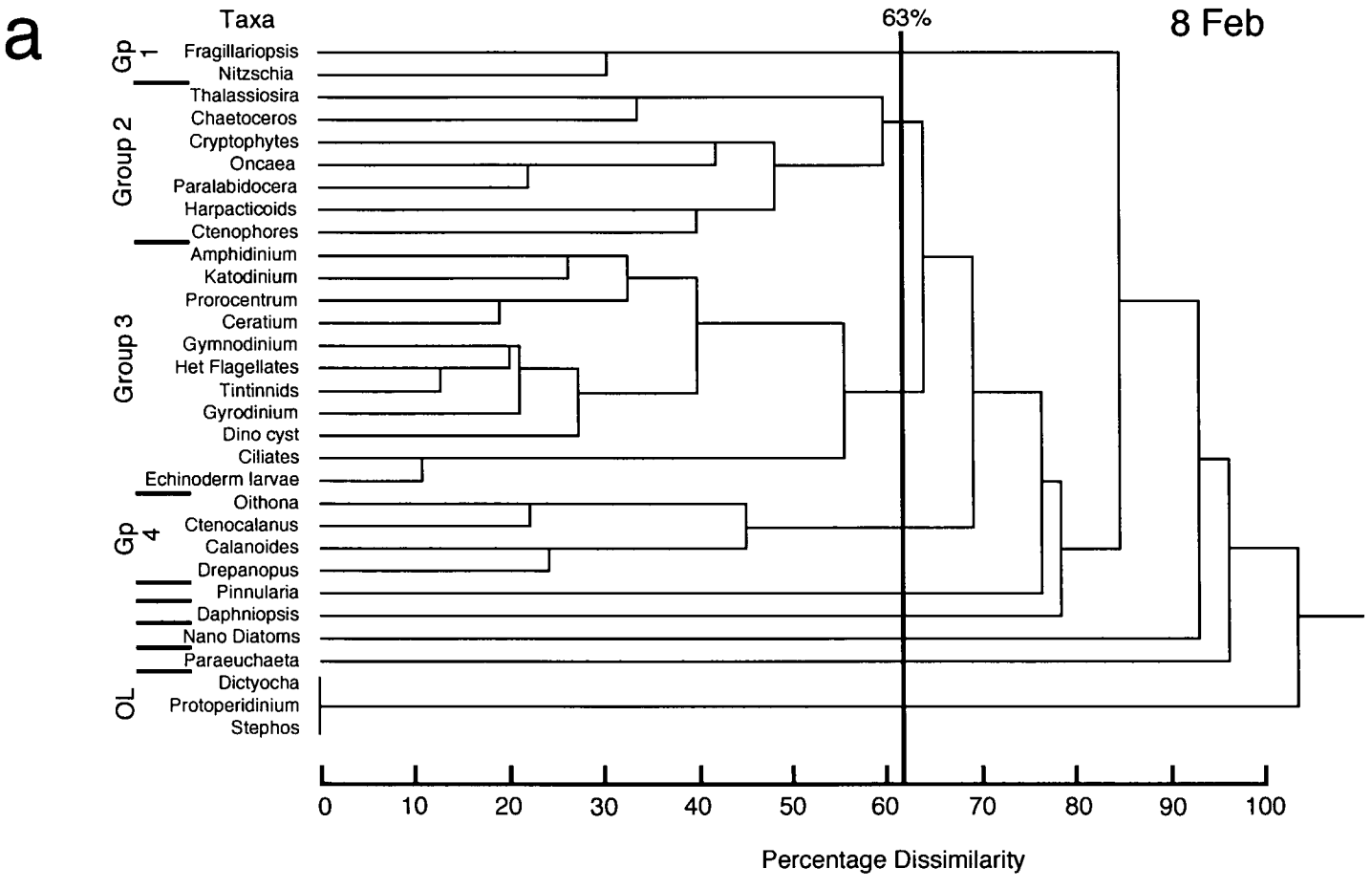


Figure A3.10a. Multivariate analysis of species associations at all depths on 8 February shows the dendrogram of cluster analysis based on the Bray-Curtis dissimilarity index with UPGMA linkage. Only the genera are listed, for species information refer to the text. GP = Group, OL = Outlier.

b

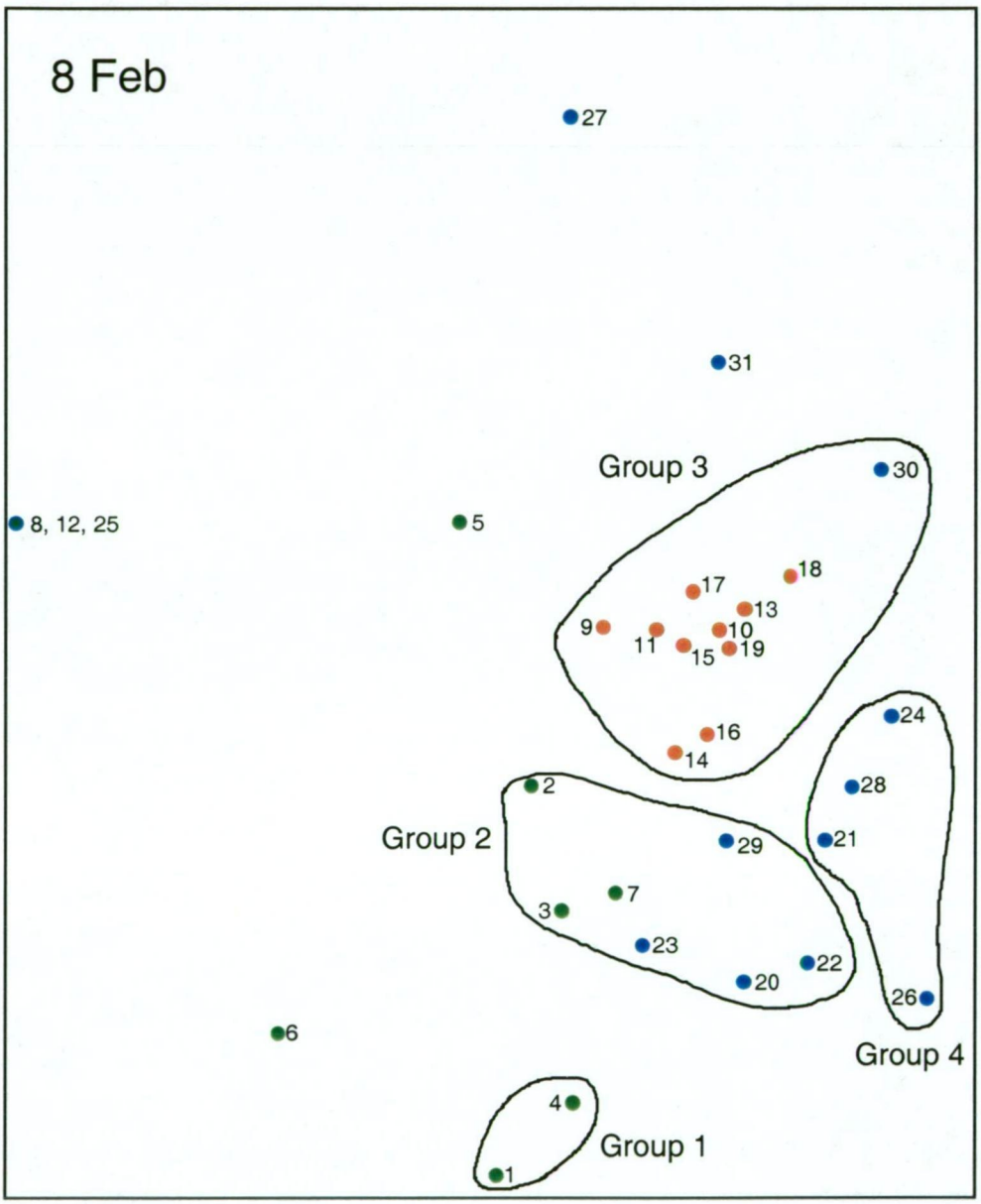


Figure A3.10b. Multivariate analysis of species associations at all depths on 8 February shows the ordination plot of the cluster analysis using NMDS. Colours denote taxa; green = phytoplankton, red = protozoa, blue = metazoa. Numbers denote species as per the text. Axis scales are not shown as they are relative in NMDS.

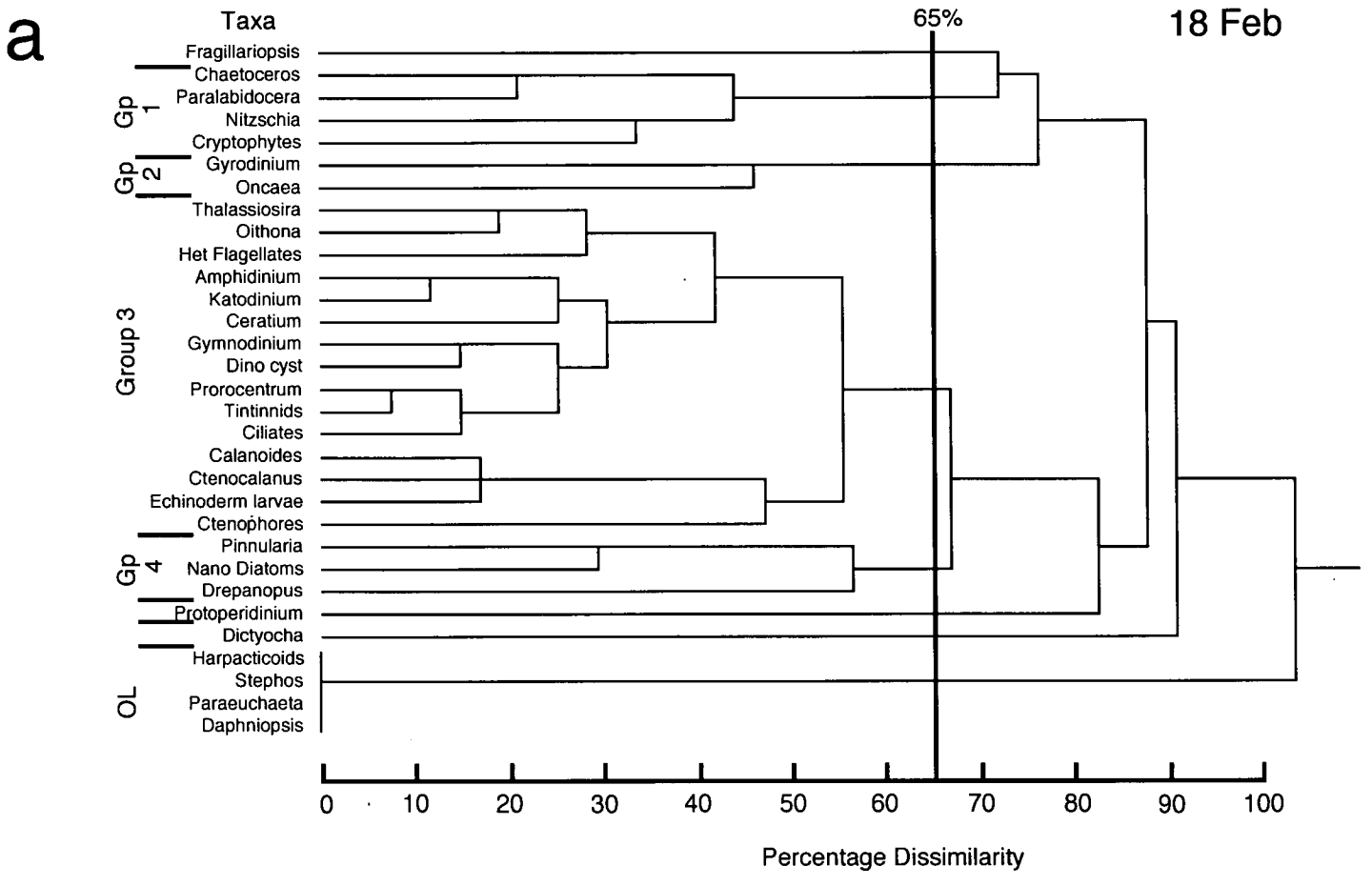


Figure A3.11a. Multivariate analysis of species associations at all depths on 18 February shows the dendrogram of cluster analysis based on the Bray-Curtis dissimilarity index with UPGMA linkage. Only the genera are listed, for species information refer to the text. GP = Group, OL = Outlier.

b

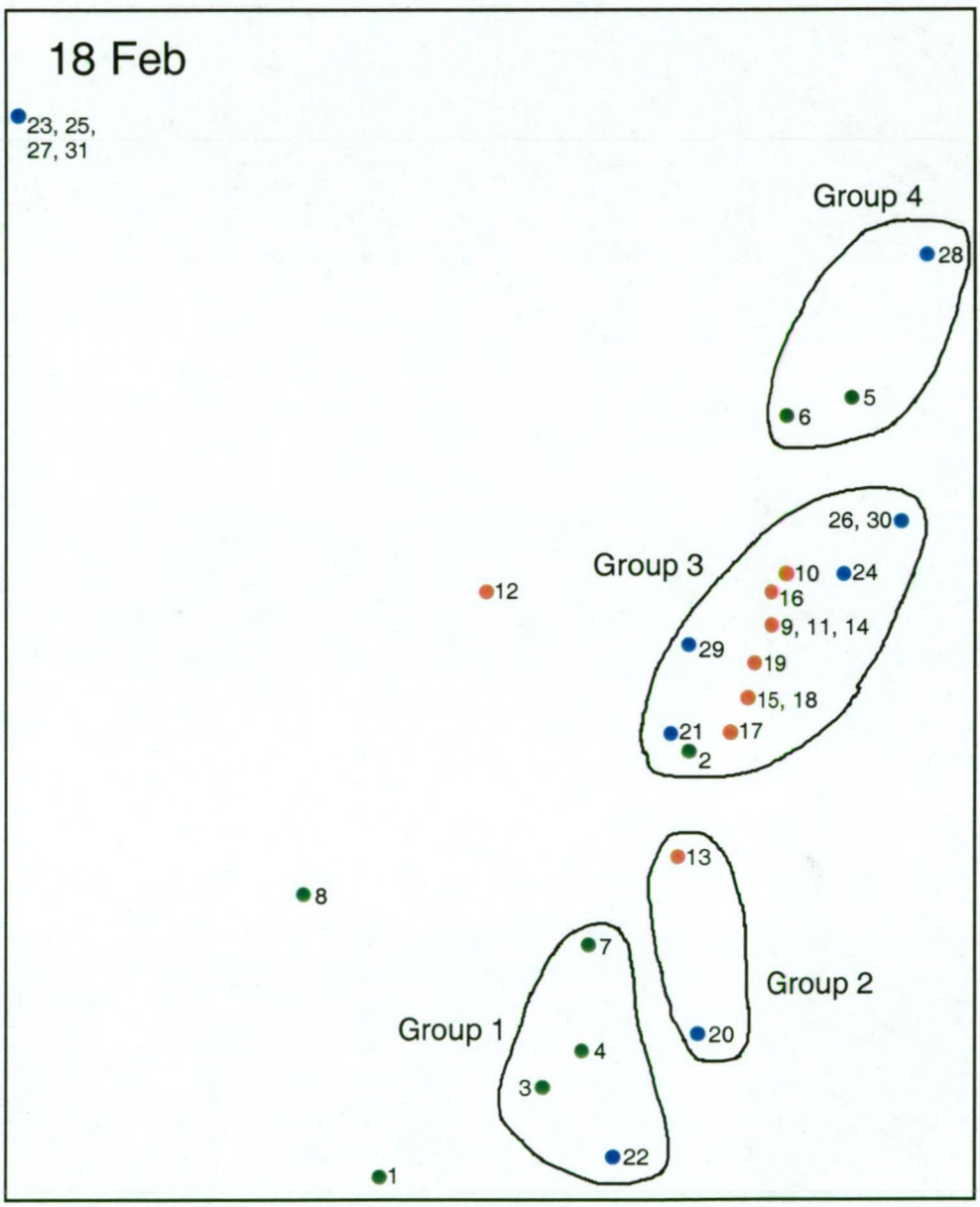


Figure A3.11b. Multivariate analysis of species associations at all depths on 18 February shows the ordination plot of the cluster analysis using NMDS. Colours denote taxa; green = phytoplankton, red = protozoa, blue = metazoa. Numbers denote species as per the text. Axis scales are not shown as they are relative in NMDS.

Appendix 4

Table A4.1. Mean protistan cell biovolume, and the carbon content per cell as calculated using Equations 6.1 & 6.2.

Species	Mean cell biovolume (μm^3)	pg C $cell^{-1}$
Fragilariopsis spp. & *F.curta* & *F.cylindrus*	617	53
Thalassiosira spp. & *T.ambigua* & *T.tumida*	785	64
Chaetoceros spp.	4700	274
Nitzschia spp. & *Pseudonitzschia subcurvata*	485	43
Amphidinium spp.	1725	236
Gymnodinium spp. & *Polarella glacialis*	4156	540
Cryptophytes incl. *Geminigera cryophyllum*	381	57
Heterotrophic flagellates & statocysts	107	17
Protoperidinium spp.	3833	501
Ciliate sp.1	122804	12979
Ciliate sp.2	15271	1833
Ciliate sp.3 cf *Strombidium* spp.	6827	861
Gyrodinium spp.	48858	5462
Prorocentrum spp.	16890	2015
Tintinnids	204507	20951
Dinoflagellate cysts	1298	181
Katodinium sp.	105872	11291
Pinnularia spp. & *Pinnularia quadratarea* v. *constricta*	17598	799
Dictyocha speculum	9087	1126
Ceratium spp.	1829	250
Entomoneis kjellmanii	3303	206
Coscinodiscus spp.	56246	2050
Pleurosigma spp.	41823	1612
Nanoplanktonic diatoms (*Fragillariopsis pseudonana*)	80	10

MARINE ECOLOGY
PROGRESS SERIES

Reprint

Inter-Research
Nordbünte 23, D-21385 Oldendorf/Luhe, Germany
Tel: (+49) 4132 7127 Fax: (+49) 4132 8883
E-mail: ir@int-res.com Internet: www.int-res.com

Vol. 245: 133–148, 2002 | MARINE ECOLOGY PROGRESS SERIES Mar Ecol Prog Ser | Published December 18

Ultrastructure, morphology and flux of microzooplankton faecal pellets in an east Antarctic fjord

Karin L. Beaumont[1,2,*], Geraldine V. Nash[2], Andrew T. Davidson[2]

[1]School of Zoology, University of Tasmania, Hobart, Tasmania, Australia
[2]Australian Antarctic Division, Channel Highway, Kingston, Tasmania, Australia

ABSTRACT: Small copepods and protozoa are major contributors to heterotrophic biomass in Antarctic waters. They produce small (<300 µm) faecal pellets, the fates of which are largely unknown. We examined the distribution and abundance of microzooplankton and small faecal pellets in Ellis Fjord, east Antarctica. We determined statistical relationships between the abundance of microzooplankton and pellets, and examined pellet morphology and ultrastructure using light and scanning electron microscopy. Our results indicate species-specific differences in the morphology and fate of pellets produced by small copepods: *Oithona similis* and harpacticoid pellets were retained in upper waters, while *Oncaea curvata* and *Paralabidocera antarctica* pellets sank to depth. Protozoan pellets did not sink to depth irrespective of their source or morphology and despite the fact they can be larger than those produced by small copepods. The majority of microzooplankton pellets, composed of phytoplankton that otherwise may have directly sedimented to depth, was retained in near surface waters and probably recycled and remineralised. Despite producing faecal aggregates, heterotrophic activity of most microzooplankton do not contribute to vertical flux but instead support respiration of matter in upper waters. This may reduce the vertical flux of particulate matter to depth, thereby reducing the capacity of Antarctic waters to act as a carbon sink, with implications for global climate.

KEY WORDS: Faecal pellets · Flux · Copepods · Protozoa

INTRODUCTION

The transfer and vertical flux of photosynthetically fixed carbon in the oceans influences atmospheric-ocean carbon flux and consequently global climate (Falkowski et al. 1998, Rivkin & Legendre 2001). Zooplankton play an important role in carbon cycling by packaging planktonic material into faecal pellets that contribute to respiration and nutrient regeneration, or vertical flux (Noji 1991, Banse 1995, Le Fèvre et al. 1998, Wassmann 1998, Turner 2000). However, the contribution by proto- and metazoa to vertical flux, particularly by individual species, is poorly understood. Small copepods have recently been recognised as being highly abundant in Antarctic waters, contributing significantly to zooplankton biomass and production (Fransz & González 1995, Swadling et al. 1997, Metz 1998, Atkinson & Sinclair 2000). Protozoa are fundamental to the function of the microbial loop, through which most of the carbon flows in marine ecosystems (Fenchel 1988, Froneman & Perissinotto 1996, Azam 1998). The production of pellets by small copepods has been recognised for some time and these pellets are reportedly respired in near-surface waters (Smetacek 1980, Wassmann et al. 1994, Bathmann 1996, González et al. 2000). In contrast, the production and flux of protozoan pellets have only recently been considered despite the fact that they can be of equivalent size to those produced by small copepods (Buck & Newton 1995, Gowing et al. 2001).

To better understand the regulation of pellet flux it is necessary to determine the ecology and tropho-

*Present address: Kingston.
Email: karin.beaumont@aad.gov.au

dynamics of key species (Verity & Smetacek 1996, Wassmann 1998, MZC2 2001). Studies investigating vertical flux using sediment traps have seldom simultaneously determined the plankton in the overlying water column. This has led to classification of faecal pellets being ill defined and their origins being largely unknown or presumed.

Marine environments that have low species richness, such as Ellis Fjord, provide the opportunity to investigate fine-scale interactions and the role of key species in vertical flux (Trull et al. 2001). In this study, we investigate the distribution, abundance and linkage between microzooplankton and small pellets, from Ellis Fjord, east Antarctica. We examine the morphology and ultrastructure of faecal pellets using light and scanning electron microscopy, and consider the extent to which species-specific trophodynamics and pellet ultrastructure affect the contribution by microzooplankton to vertical flux.

METHODS

Study site and field sampling. This study was conducted in an east Antarctic fjord, Ellis Fjord (68.5° S, 78.0° E) in the Vestfold Hills. The fjord is approximately 10 km long and 1 km wide, and contains 5 major basins. Our sampling site was located in Middle Basin, which has a maximum depth of approximately 80 m. The majority of the fjord has remained ice-covered since 1991 (McMinn 1994, Gibson 1999). While the fjord was ice-covered during this study (December 1997 to March 1998), we observed substantial surface and under-ice melt. Detailed descriptions of the physico-chemical characteristics of the fjord are provided by Gibson (1998, 1999). The seasonal succession of the plankton community at the study site forms a separate study (Beaumont et al. unpubl.).

Holes were drilled in the sea-ice using a 20 cm auger attached to a Jiffy drill. A 100 µm mesh umbrella net with a mouth of 28 × 28 cm (Kirkwood & Burton 1987) was deployed to sample the zooplankton community. Net hauls were taken from 5, 10, 20 and 40 m to surface at each of 3 holes in the ice, thereby providing 3 independent replicate hauls for each depth. The samples were preserved in Steedman's solution containing 5% buffered formalin, 4.5% propylene glycol, and 0.5% propylene phenoxytol (Steedman 1976).

A 2 l Kemmerer bottle was used to obtain water samples at approximately weekly intervals to examine the protistan community in the water column. Three replicate samples were taken at 5, 10, 20 and 40 m. The sample was transferred to a 2 l polycarbonate jar, placed in a dark, insulated container, and transported to the laboratory.

Sediment traps were deployed through 20 cm diameter holes drilled through the ice cover of the fjord. The traps consisted of a cylindrical section (internal diameter 65 mm, 6:1 aspect ratio) connected to a funnel that tapered into a cylindrical collector tube after Bloesch & Burns (1980) and Rosa et al. (1994). The traps were filled with 0.2 µm filtered seawater to which 50 g l^{-1} sodium chloride and 6.5×10^{-4} g l^{-1} mercuric chloride had been added to minimise loss of material during retrieval and *in situ* bacterial production (Knauer et al. 1984, Lee et al. 1992). Three replicate traps were suspended at depths of 5, 10, 20 and 40 m in the water column and samples were obtained weekly. For further details regarding the field-sampling regime, see Beaumont et al. (2001). The fixed samples, containing faecal pellets, were analysed in the laboratory upon return to Australia.

We attempted to measure current speeds at the study site using flowmeters, but problems with ice conditions (clogging of the meter) and the stability of the vane rendered the data unreliable. High flow rates have been recorded through the narrow seaward entrance to the fjord where the ice often melts completely during summer leaving this entrance exposed to wind-induced turbulence (Kirkwood 1993). However, the flow rate at the landward entrance is low and the ice rarely melts completely. Our study site was located towards the landward end of the fjord and remained ice-covered throughout summer, so turbulence was likely to be low during this study.

Laboratory methods. Net haul samples were examined using a dissecting microscope. The dominant metazoa were identified and counted. Metazoan abundance was calculated using the mouth area of the net and the vertical distance towed, assuming 100% filtration efficiency. The mean and SE of the 3 replicate samples were determined. However, where samples were lost and there were less than 3 replicate samples, no SE were calculated. The mean abundances were then subtracted from consecutive depths to determine abundance at the following depth intervals: 0–5, 5–10, 10–20, and 20–40 m.

Each 2 l water sample was mixed, and a 500 ml aliquot from each replicate Kemmerer bottle sample was decanted into a measuring cylinder and fixed with acid Lugol's iodine. Samples were left for approximately 24 h and then the supernatant was removed by aspiration. The remaining sample (approximately 50 ml) was transferred to a glass, screw-lidded container and refrigerated at 0 to 4°C prior to microscopic analysis.

Protozoa were settled in Utermöhl sedimenting chambers, identified and counted using an inverted microscope. Only samples taken during January and February were analysed, as chlorophyll *a* (chl *a*) con-

centration in the water column indicated peak biomass during these months (Beaumont unpubl.). Two independent replicate samples were analysed for each sampling date. Fifteen replicate fields (or portions thereof) were counted per sample and the mean and SE calculated. Dinoflagellates were grouped as autotrophic or heterotrophic by the presence of chlorophyll under transmitted light, starch storage products, and the trophic status according to Tomas (1996). Mixotrophic species were included as protozoa.

Sediment trap samples were left to settle as above and examined using an inverted microscope to identify and enumerate faecal pellets. Faecal pellets were classified into 4 categories based on pellet descriptions from the literature: cylindrical, oval, pellets with intact frustules, and minipellets (Urrère & Knauer 1981, Gowing & Silver 1985, González 1992a,b, González et al. 1994a, Buck & Newton 1995). Subsamples were taken and pellet concentration determined for each replicate, and the grand mean count was calculated. The maximum and minimum values for the 2 replicate samples were used to indicate the variance between traps.

Statistical analyses. Plankton were progressively integrated throughout the overlying water column to corresponding trap depths for the entire summer season. The data were transformed using the log $(x+1)$ transformation to account for heterogeneity and to normalise the distributions in the data. Linear regressions were performed between the integrated abundance of plankton (m^{-2}) in the overlying water column and the flux of faecal pellets (m^{-2} d^{-1}) to traps at each depth (i.e. the faecal pellet abundance at 40 m was regressed against the plankton abundance from 20–40, 10–40, 5–40 and 0–40 m). The correlation coefficient was used to determine the statistical significance of these relationships.

Microscopy. To obtain a representative cross-section of pellet types throughout the season, weekly samples were pooled for the examination of pellet morphology and ultrastructure.

Whole faecal pellets: Faecal pellets were isolated by micro-pipette and transferred to a droplet of 0.2 µm filtered seawater. The water containing the pellet was mixed and the isolation repeated until the pellet was free from extraneous organic matter. Faecal pellets were then separated according to their morphology, and photographed under natural light at 400× magnification using a Leitz Fluovert inverted microscope.

Various methods were used to minimise disruption of the faecal pellets during preparation for scanning electron microscopy (SEM). Oval and minipellets were pipetted onto 25 mm diameter Nuclepore filters (5.0 µm pore size) and blotted to remove excess water. A subsample of an entire trap sample that contained faecal pellets and other matter was also pipetted directly onto a Nuclepore filter to examine the complete array of pellets in the trap. Pellets containing whole diatom frustules, were pipetted onto glass microscope slides that had been coated with polylysine (Marchant & Thomas 1983). Cylindrical pellets were pipetted into a Nuclepore filter 'basket' that consisted of 2 layers of filter paper wedged between magnet rings. The filters and slides with attached samples were placed in petri dishes, gently washed with 10% ethanol to remove traces of mercuric chloride, and fixed with osmium tetroxide vapour. They were then dehydrated through a graded ethanol series followed by a concentrated solution of hexamethyl disilizane, and dried in a fume hood. The samples were subsequently mounted on carbon tabs with silver paint, and then on stubs, sputter coated with gold, and examined by SEM.

Faecal pellet contents: Faecal pellets had been preserved in mercuric chloride that reportedly inhibits bacterial ectoenzyme activity in seawater (Christian & Karl 1995). However, the extent to which mercuric chloride penetrates the faecal pellet is unknown. Pellets with membranes that masked the pellet contents were rinsed and pipetted into 0.2 µm filtered seawater and placed in an oven at 20°C for 24 h to allow for potential microbial stripping of the membrane (Turner 1984). In the event that microbial stripping did not occur, we concurrently adapted a method used to clean diatom frustules and placed pellets in 50% hydrogen peroxide for 2 to 3 d (Battarbee 1986). All pellets were subsequently pipetted onto Nuclepore filters and prepared for SEM (see above).

RESULTS

Plankton

This study examined the distribution and abundance of micro-pellets and their relationship with the dominant plankton in the water column. Several copepod species (*Ctenocalanus citer* Heron & Bownman, *Drepanopus bispinosis* Bayly, *Stephos longipes* Giesbrecht and *Paraeuchaeta antarctica* Giesbrecht), a larvacean, and echinoid larvae were not included in our analyses due to their low or brief periods of abundance. In addition, pellets typical of the large, common, Antarctic copepod *Calanoides acutus* Giesbrecht were not observed; the morphology of pellets produced by ctenophores is unknown (Reeve & Walter 1978), and pellets produced by heterotrophic nanoflagellates are reportedly too small (approximately 1 µm) to be detected by the methods used in this study (Elbrachter 1991). Therefore, these plankton taxa are not considered any further.

Small copepods were abundant throughout this study, especially in the upper 20 m of the water column, and showed extremely high spatial variability (SE from 1 to 100% of the mean) (Table 1). *Oncaea curvata* was the dominant copepod (Fig. 1a, Table 1). This species increased in abundance during December to peak in January, but declined in February and March (Fig. 1a). *Paralabidocera antarctica*, *Oithona similis* and harpacticoid copepods were in much lower abundance than *O. curvata* (averaging <30 m^{-3}) (Fig. 1a,b). *P. antarctica* was present throughout December and January, but declined in February and was absent in March. In contrast, *O. similis* peaked during February and early March while harpacticoids exhibited a brief peak in mid January (Fig. 1b).

Table 1. Mean abundance of copepods (ind. m^{-2}, mean ± SE) at depth intervals from surface to 40 m. *<3 replicate samples where no SE was calculated

Date[a]	0–5 m	0–10 m	0–20 m	0–40 m
Oncaea curvata				
16/12/97	0*	94 ± 32	232 ± 91	325*
23/12/97	281 ± 141	957 ± 145	1257 ± 52	1790 ± 26
28/12/97	212 ± 153	991 ± 283	2934 ± 1046	3900 ± 1314
4/1/98	434 ± 124	1967 ± 275	4344 ± 887	4443 ± 1386
11/1/98	592 ± 217	1208 ± 401	4739 ± 690	4566 ± 1750
18/1/98	128 ± 32	735 ± 223	2505 ± 226	3826 ± 408
25/1/98	10 ± 10	108 ± 51	789 ± 256	2199 ± 403
1/2/98	64 ± 10	74 ± 31	680 ± 157	1425 ± 43
8/2/98	79 ± 20	44 ± 9	1045 ± 156	1637 ± 590
18/2/98	79 ± 18	49 ± 13	104 ± 39	1755 ± 271
4/3/98	59 –	35 ± 5	192 ± 31	986 ± 124
Paralabidocera antarctica				
16/12/97	22*	15 ± 9	0 –	0*
23/12/97	79 ± 30	84 ± 18	5 ± 5	20 ± 5
28/12/97	30 ± 30	35 ± 18	20 ± 13	20 ± 10
4/1/98	69 ± 30	64 ± 18	69 ± 25	64 ± 36
11/1/98	5 ± 5	25 ± 5	54 ± 18	20 ± 13
18/1/98	30 ± 15	84 ± 13	182 ± 21	138 ± 13
25/1/98	15 ± 9	15 ± 15	30 ± 23	99 ± 30
1/2/98	30 ± 15	44 ± 30	84 ± 35	99 ± 44
8/2/98	0 –	0 –	54 ± 30	84 ± 10
18/2/98	5 ± 5	5 ± 5	5 ± 5	10 ± 5
4/3/98	0 –	0 –	0 –	0 –
Oithona similis				
16/12/97	0*	0 –	10 ± 10	15*
23/12/97	25 ± 10	5 ± 5	10 ± 10	35 ± 18
28/12/97	5 ± 5	5 ± 5	10 ± 5	35 ± 18
4/1/98	5 ± 5	15 ± 9	20 ± 13	59 ± 17
11/1/98	25 ± 5	35 ± 18	123 ± 75	123 ± 101
18/1/98	49 ± 35	69 ± 10	108 ± 32	104 ± 15
25/1/98	20 ± 5	44 ± 15	49 ± 26	49 ± 20
1/2/98	64 ± 13	74 ± 48	242 ± 25	217 ± 39
8/2/98	35 ± 5	39 ± 13	222 ± 112	237 ± 87
18/2/98	20 ± 13	49 ± 42	104 ± 17	25 ± 25
4/3/98	0 –	64 ± 13	148 ± 30	375 ± 49
Harpacticoids				
16/12/97	0*	0 –	0 –	0*
23/12/97	0 –	0 –	0 –	0 –
28/12/97	0 –	0 –	0 –	0 –
4/1/98	15 –	10 ± 10	0 –	0 –
11/1/98	0 –	0 –	5 ± 5	0 –
18/1/98	64 ± 10	25 ± 10	84 ± 40	39 ± 13
25/1/98	25 ± 10	44 ± 15	20 ± 10	10 ± 10
1/2/98	0 –	30 ± 9	15 –	5 ± 5
8/2/98	0 –	5 ± 5	20 ± 10	0 –
18/2/98	0 –	0 –	0 –	0 –
4/3/98	0 –	0 –	0 –	0 –

[a]Dates given as d/mo/yr

Heterotrophic dinoflagellates (HDIN) were in low concentration throughout January, but increased to a peak concentration of 6.33 ± 0.66 × 10^7 m^{-3} at ≤5 m in early February (Fig 1c). HDIN concentration was similarly high between 5 and 10 m at this time, while the concentration at ≥20 m depth increased later in the month. Mixotrophic *Ceratium* spp. dominated the HDIN taxa, however *Gyrodinium* spp., and *Katodinium* spp. contributed to the HDIN concentration during late summer. *Amphidinium* spp. and *Protoperidinium* spp. were also present in low concentrations but reached maximum concentrations on 18 February of 8.92 ± 1.35 × 10^6 m^{-3} between 10 and 20 m, and 4.54 ± 3.63 × 10^6 m^{-3} between 20 and 40 m respectively. *Gymnodinium* spp. were also abundant, but it is likely that most of the species we observed were autotrophic as the cells contained chloroplasts. Therefore, the abundance of this taxon was not included in the total HDIN abundance.

Ciliates comprised *Strombidium* spp., oligotrich genera, and tintinnids. The concentration of ciliates was much lower than that of HDIN but showed a similar temporal pattern of abundance. Ciliate concentration was low throughout January but increased in the upper 10 m in mid-February, with the peak concentration of of 3.96 ± 0.38 × 10^7 m^{-3} at ≤5 m (Fig. 1c). However, in contrast to that of HDIN, ciliate concentration at depths ≥20 m remained low throughout the season. Overall, the concentration of both HDIN and ciliates was highly variable (Fig. 1c).

Faecal pellets

Cylindrical pellets were most abundant from December to January, with a peak

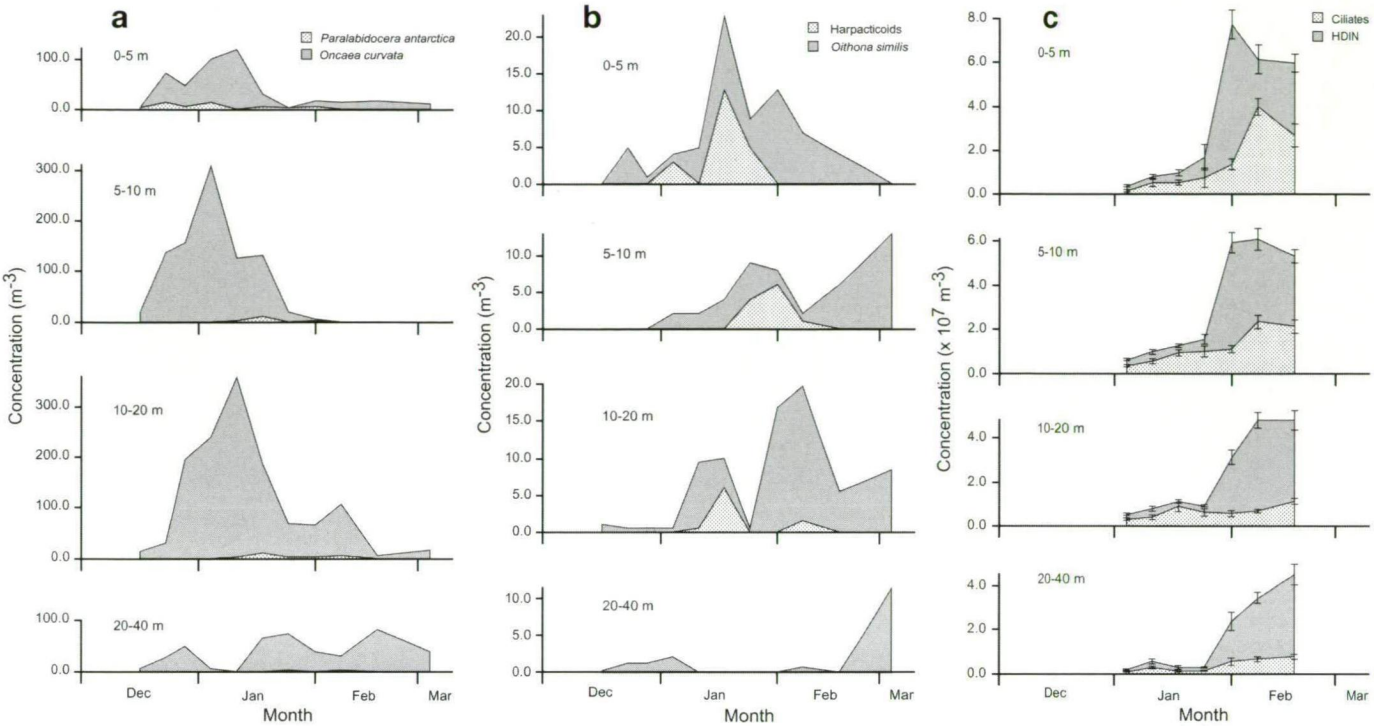


Fig. 1. Abundance of (a) *Oncaea curvata* and *Paralabidocera antarctica*, (b) *Oithona similis* and harpacticoids, and (c) heterotrophic dinoflagellates (HDIN) and ciliates (error bars represent ± 1 SE) in the water column

flux of $1.20 \pm 0.70 \times 10^4$ pellets m^{-2} d^{-1} observed at 40 m, but generally declined during February and March (Fig. 2a). Oval pellets dominated total pellet flux with a sedimentation peak of $5.24 \pm 1.54 \times 10^5$ pellets m^{-2} d^{-1} recorded at 5 m in late January. Sedimentation of these pellets persisted until late February in the upper 10 m of the water column. The flux of oval pellets to ≥20 m in the water column was low throughout this study.

Pellets containing only intact frustules sedimented throughout most of the season, predominantly in the upper water column, reaching $1.27 \pm 0.89 \times 10^5$ pellets m^{-2} d^{-1} at 10 m in mid-January and $1.15 \pm 0.72 \times 10^5$ pellets m^{-2} d^{-1} in early February. In contrast, minipellets showed only a brief period of sedimentation in the water column in mid February (Fig. 2b). In general, the flux of minipellets to ≤20 m was low and highest flux was observed at 40 m ($2.92 \pm 0.53 \times 10^5$ pellets m^{-2} d^{-1}).

Table 2. Significant correlations (all positive) between plankton species and pellet types

Organism	Pellet type	Water column above trap depth	Trap depth	r	n	Probability
Oithona similis	Cylindrical	0–5	5	0.656	11	$0.02 < p < 0.05$
	Minipellets	10–20	20	0.622	11	$0.02 < p < 0.05$
Harpacticoids	Minipellets	5–40	40	0.641	11	$0.02 < p < 0.05$
HDIN	Minipellets	0–10	10	0.754	7	$0.02 < p < 0.05$
	Minipellets	5–10	10	0.798	7	$0.02 < p < 0.05$
	Minipellets	0–20	20	0.920	7	$0.002 < p < 0.005$
	Minipellets	5–20	20	0.913	7	$0.002 < p < 0.005$
	Minipellets	10–20	20	0.890	7	$0.02 < p < 0.05$
Ciliates	Minipellets	0–10	10	0.876	7	$0.005 < p < 0.01$
	Minipellets	5–10	10	0.827	7	$0.02 < p < 0.05$

Plankton and faecal pellet correlations

While most plankton taxa did not correlate with the abundance of pellets in traps, significant correlations were observed between microzooplankton taxa and pellet types (Table 2).

The abundance of *Oncaea curvata* and *Paralabidocera antarctica* from early to mid summer (December to January) coincided with the flux of cylindrical faecal pellets in the water column. In particular, the occurrence of pellets at 40 m resembled the abundance of these species of plankton between 10 and 20 m (Figs. 1a & 2a). No significant correlations were observed between the abundance of these species and that of

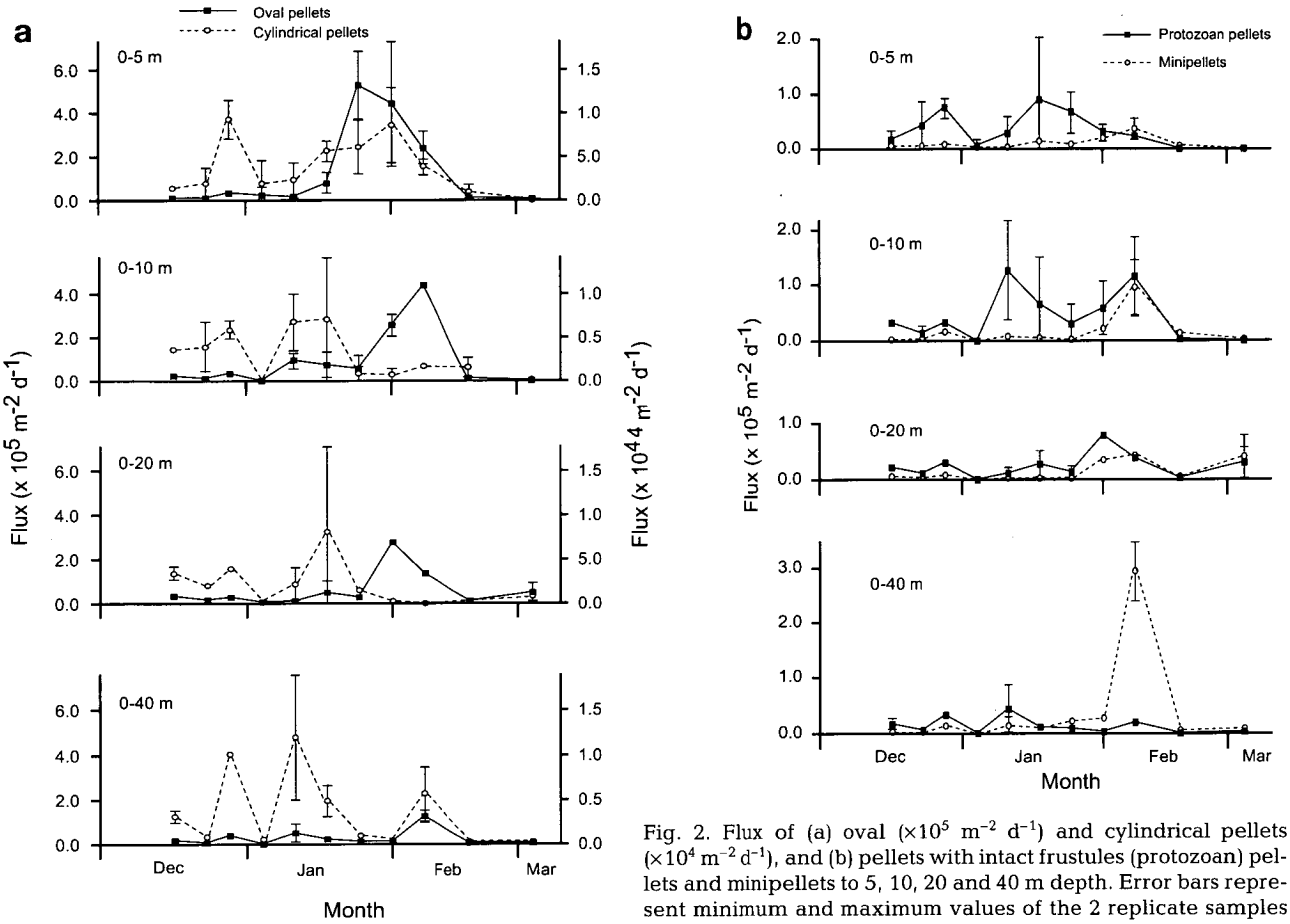


Fig. 2. Flux of (a) oval ($\times 10^5$ m^{-2} d^{-1}) and cylindrical pellets ($\times 10^4$ m^{-2} d^{-1}), and (b) pellets with intact frustules (protozoan) pellets and minipellets to 5, 10, 20 and 40 m depth. Error bars represent minimum and maximum values of the 2 replicate samples

cylindrical pellets. However, the abundance of *P. antarctica* between 5 and 10 m and the flux of cylindrical pellets to 10 m showed a relationship that approached significance ($0.05 < p < 0.10$).

The abundance of *Oithona similis* and harpacticoids in late January and February coincided with the flux of oval pellets in the water column (Figs. 1b & 2a), and near-significant correlations were observed between the two ($0.05 < p < 0.10$). *Oithona similis* and harpacticoids at ≥20 m significantly correlated with the flux of minipellets to 20 and 40 m respectively (Table 2), and the abundance of *O. similis* in the upper 5 m showed a near-significant correlation with the flux of minipellets to 5 m ($0.05 < p < 0.10$). Furthermore, the abundance of *O. similis* showed a consistent, but not significant, negative relationship ($-0.989 < \text{slope} < -0.831$) with the abundance of cylindrical pellets at depth intervals throughout the water column (data not shown), except at ≤5 m where we observed a significant positive correlation between *O. similis* and cylindrical pellets.

Heterotrophic dinoflagellates were most abundant from mid to late summer, and pellets with intact frustules were abundant in traps throughout the season (Figs. 1c & 2b). While both the concentration of organisms and the flux of pellets were greatest in the upper 10 m of the water column, they were not significantly correlated ($p > 0.2$). In contrast, the concentration of HDIN at depth intervals ≤20 m significantly correlated with the flux of minipellets to traps at 10 and 20 m depths.

The abundance of ciliates in the upper 10 m of the water column in mid February coincided with an abundance of minipellets, and a significant correlation was observed between the two at ≤10 m.

Faecal pellet morphology and ultrastructure

Nine different faecal pellet types were discriminated on the basis of their morphology and ultrastructure (Table 3).

Cylindrical pellets

Cylindrical pellets largely contained diatom fragments with no interstitial connective material, but some whole frustules of *Thalassiosira* sp., *Nitzschia*

Table 3. Types, sizes, contents and probable origin of faecal pellets in sediment traps throughout the upper 40 m of the water column during summer in Ellis Fjord. Where pellet sizes were consistent the dimensions were averaged. Pellets varying greatly in size are presented as ranges. Ø: diameter, MB: membrane bound, DF: fragmented diatom frustules, WD: whole diatom frustules, + or – CM: with or without interstitial connective material

Pellet type	Average or range in size (µm)	Contents	Probable origin
Cylindrical	250 × 73	MB, DF, –CM	*O. curvata* and *P. antarctica*
Oval	80 × 60 to 190 × 155	MB, WD and DF, cysts, +CM	*O. similis* and harpacticoids
Intact frustules			
Oval	150 × 110	MB, WD of single or multi-species –CM	Athecate dinoflagellates
Irregular	130 × 120	MB, WD of single species, –CM	Phagotrophic dinoflagellates
Round	150–250 Ø	MB, WD of single species, –CM	Pallium-feeding dinoflagellates
Minipellets			
Oval	25 × 18 to 60 × 35	±MB, DF < 10 µm, detritus and crushed material	Dinoflagellates and ciliates
Spherical	60–80 Ø	MB, DF, WD > 20 µm	Copepod nauplii
Semi-transparent	30 Ø	MB, WD	Dinoflagellates
False	50 Ø	Partially MB, DF	By-product of coprophagy

stellata (Mang.) and *Nitzschia prolongatoides* (Hasle) were observed (Table 3, Fig. 3a–c). We also occasionally observed microbial degradation of the bounding membrane surrounding these pellets (Fig. 3d). Cylindrical pellets were poorly retained on standard Nuclepore filters and polylysine coated microscope slides, and had to be contained in a filter 'basket' during preparation for SEM.

Oval pellets

Oval faecal pellets were densely packed, membrane bound and varied considerably in size (Table 3, Fig. 3e,f). These pellets largely contained fragmented frustules of *Fragillariopsis curta* (Van Heurek) Hustedt and *Fragillariopsis cylindrus* (Grunow) Krieger (Fig. 3g). However, oval pellets also contained filamentous threads and organic matter in the interstitial spaces between frustules (Fig. 3g), and occasional whole diatom frustules, dinoflagellate cysts, and chryosphyte statocysts. Whole frustules were also observed adhered to the outer surface of the pellet (Fig. 3h). The pellets were resilient during handling and preparation in the laboratory, and the membrane remained largely intact after microbial stripping.

Faecal pellets with intact frustules

Three types of membrane-bound faecal pellets containing intact, empty frustules were evident by light microscopy (LM) (Table 3, Fig. 4a–e). Oval pellets contained either 1 species of diatom (often chain-forming) (Fig. 4a,b), or a variety of intact pennate and centric diatom frustules (Fig. 4c). Irregular and round pellets contained frustules of a single pennate diatom species (Table 3, Fig. 4d,e). All pellets appeared semi-transparent when viewed by LM and some details of the frustules within the pellets were evident through the bounding membrane. In addition, the membrane frequently ruptured during handling and the integrity of the pellet contents was not retained (Fig. 4f).

Minipellets

Four types of minipellets were evident. It was not possible to determine whether interstitial connective material was present in minipellets. Oval and spherical minipellets appeared consolidated: pellets were opaque under LM and their contents were densely packed. Oval minipellets were observed both with and without a bounding membrane and contained detritus, crushed material and fragments of small (<10 µm long) diatoms (Table 3, Fig. 5a,b). Spherical minipellets were membrane-bound and contained diatom fragments and whole frustules >20 µm (Table 3, Fig. 5c). Semi-transparent minipellets, discriminated using LM, were small, oval to irregular in shape, membrane-bound, and contained intact pennate diatom frustules (Table 3, Fig. 5d). These pellets were not as common as consolidated minipellets under LM (Fig. 5e). Observation of a complete trap sample by SEM also showed minipellets that were partially membrane-bound (Table 3, Fig. 5f) and resembled the end of a cylindrical pellet (see Fig. 3d).

DISCUSSION

Microcopepods and protozoa are major contributors to heterotrophic biomass in the oceans (Lessard 1991,

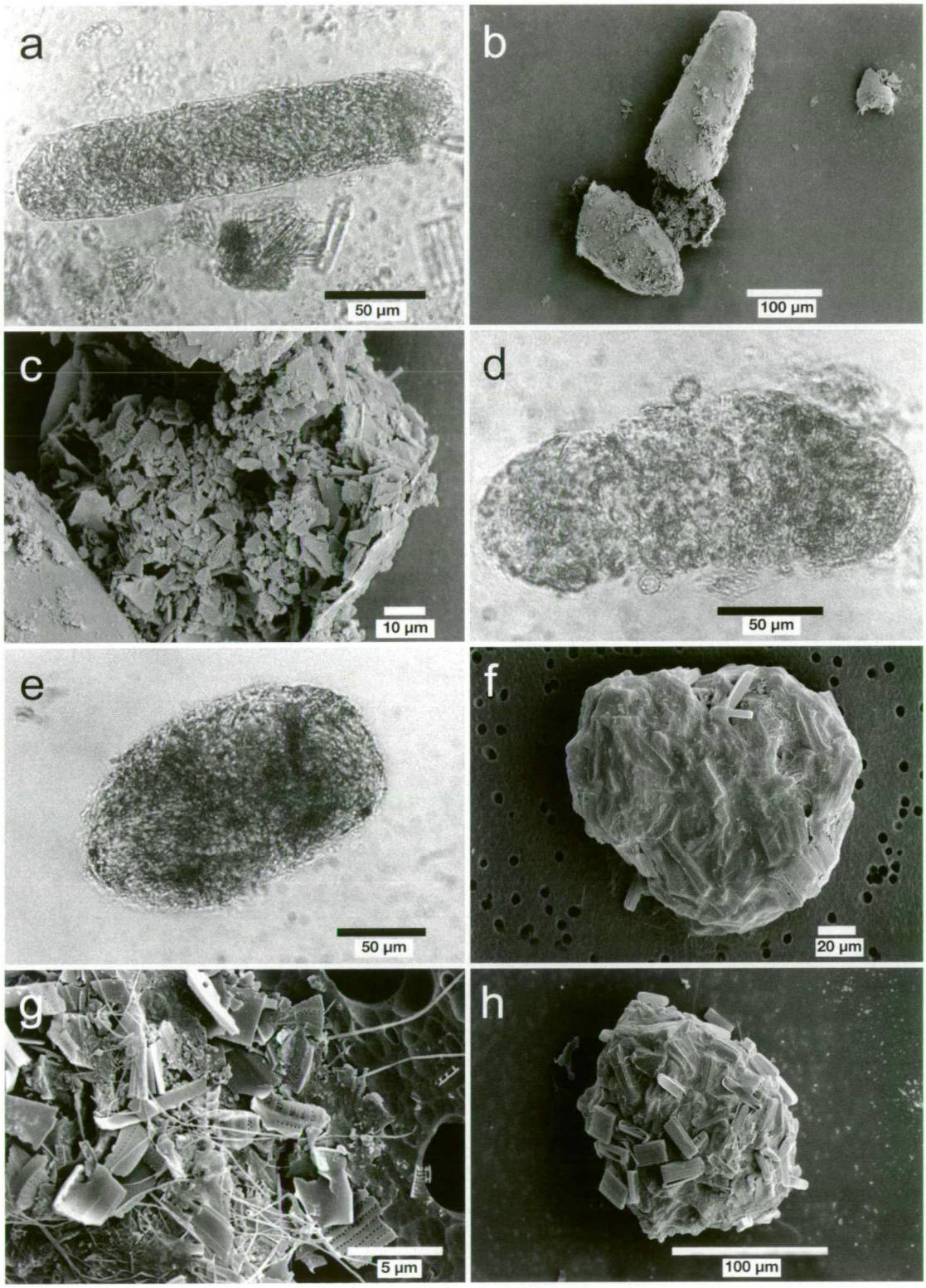


Fig. 3. Morphology and ultrastructure of cylindrical (a to d) and oval (e to h) pellets showing (a) LM of an intact cylindrical pellet with densely compacted contents, (b) SEM of a pellet broken in two, (c) SEM of pellet contents showing diatom fragments and a lack of interconnecting organic matter, (d) LM showing degradation of the bounding membrane of the pellet, (e) LM of a densely compacted oval pellet, (f) SEM of a pellet showing the shape of whole diatom frustules beneath the bounding membrane, (g) SEM of pellet contents comprising diatom fragments, whole frustules and other organic matter, and (h) SEM showing whole diatom frustules adhered to the outer surface of the pellet

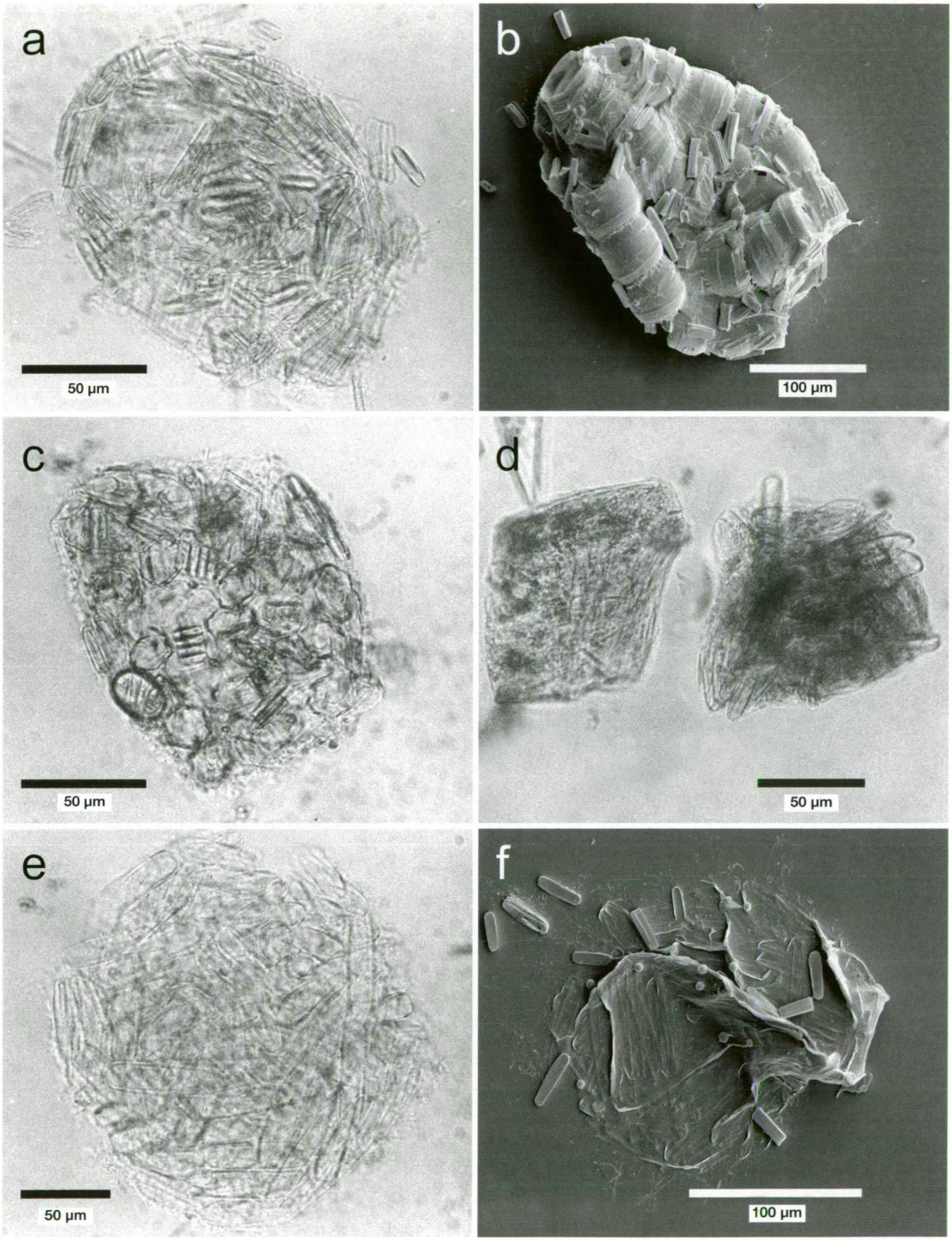


Fig. 4. Morphology and ultrastructure of pellets containing intact frustules showing (a) LM of an oval pellet containing monospecific pennate diatoms, (b) SEM of an oval pellet containing a chain of centric diatoms, probably a *Thalassiosira* sp., (c) LM of an oval pellet containing mixed diatom species, (d) LM of irregular pellets containing pennate diatoms, (e) LM of a large round pellet containing monospecific pennate diatoms, and (f) SEM of a ruptured pellet that has lost its structural integrity

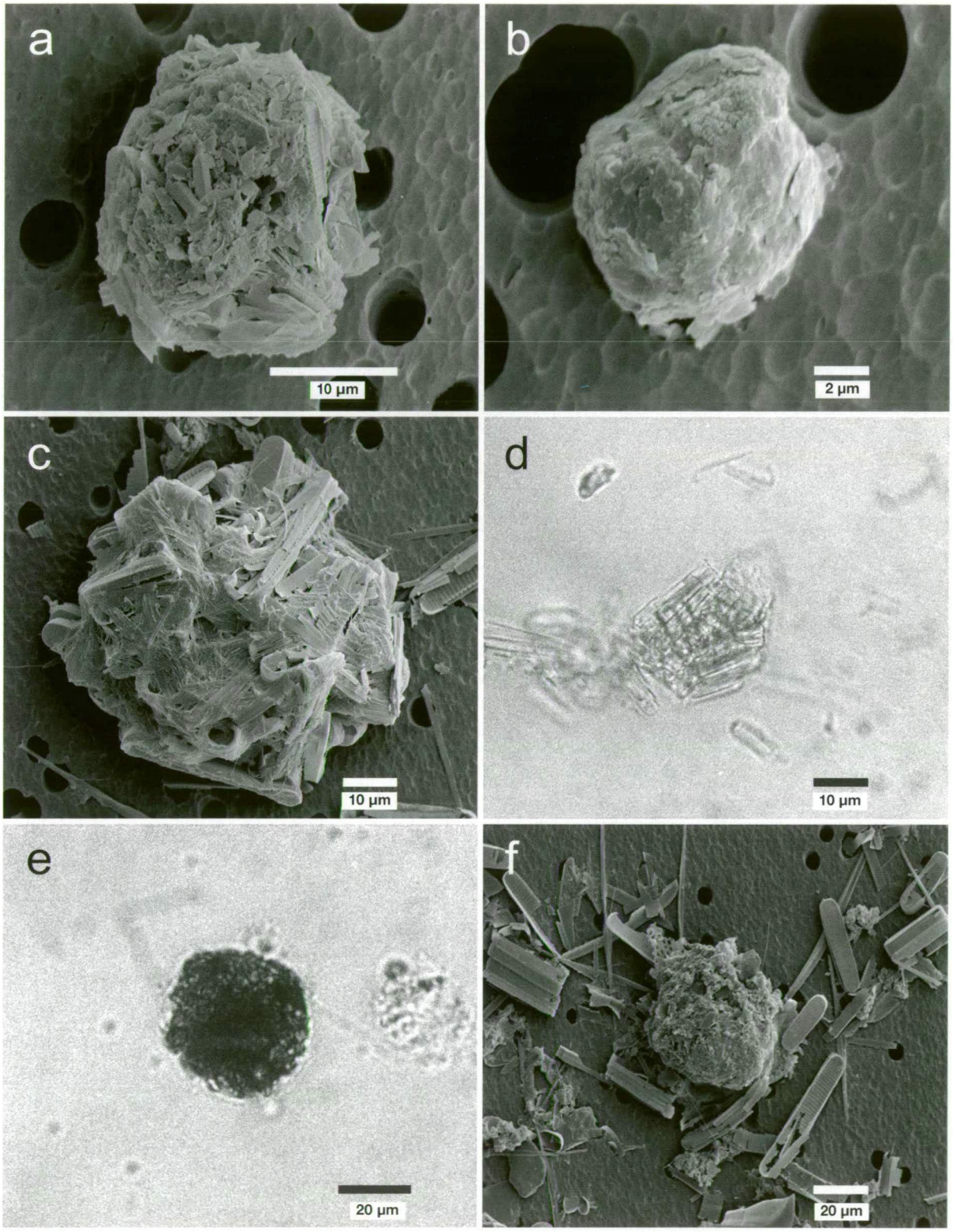


Fig. 5. Morphology and ultrastructure of minipellets showing (a) SEM of an oval consolidated minipellet comprising detritus and diatom fragments with no bounding membrane, (b) SEM of an oval consolidated minipellet with a bounding membrane, (c) SEM of a spherical consolidated minipellet comprising diatom fragments and whole frustules, (d) LM of a semi-transparent minipellet containing intact diatom frustules, (e) LM of a consolidated minipellet whose contents could not be discerned, and (f) SEM of a false minipellet that resembled the degraded end of a cylindrical pellet

Metz 1998, MZC2 2001). These microzooplankton graze much of the primary production in upper waters and contribute to particle aggregation via the production of faecal pellets (Buck et al. 1990, Garrison 1991, Verity & Vernet 1992, Metz 1998). It has been reported that particles >100 µm contribute most of the vertical carbon flux in the oceans (e.g. Fowler & Knauer 1986, Williams et al. 1989, Fortier et al. 1994). However, surprisingly little work has been done to investigate species-specific differences among microzooplankton pellets, nor their persistence in the water column and contribution to this flux. Here we examine the distribution, abundance and ultrastructure of each faecal pellet type observed in sediment traps from Ellis Fjord and determine their likely producers and fate.

While significant correlations were observed between the abundance of plankton taxa and the flux of individual pellet types, we also observed near-significant ($0.05 < p < 0.10$) relationships where the magnitude of the slope was high and consistently positive or negative with depth. This indicated a consistent relationship between individual plankton taxa and pellet flux. These near-significant correlations suggest that the linkage between plankton and the vertical flux of their faecal pellets was affected by the mediation of pellet flux by trophic processes (e.g. coprophagy and microbial degradation) and the spatial and temporal variability in plankton and pellet abundance. The vertical distribution of copepods is reportedly highly variable and no consistent pattern of diel vertical migration has been observed in Ellis Fjord (Kirkwood 1993). Swimmers can also confound relationships between plankton and pellet flux by voiding their guts upon entering poisoned traps (Harbison & Gilmer 1986). However, few swimmers were observed in trap material and *in vitro* studies of copepods (the most abundant swimmer) showed that animals did not void their guts upon contact with mercuric chloride and brine solution, nor did brine cause any herniation of copepod guts (Beaumont et al. in prep).

Cylindrical pellets

The abundance of *Oncaea curvata* and *Paralabidocera antarctica* in early summer coincided with the flux of cylindrical pellets in the water column. *P. antarctica* reportedly produces cylindrical pellets around 350 to 450 µm long (Tanimura et al. 1984). The morphology of *O. curvata* pellets is unknown, but cylindrical pellets, ranging from 70 to 260 µm in length, were produced by a temperate *Oncaea* sp. in the laboratory (Turner unpubl. data). There were no significant correlations between the abundance of these copepods and cylindrical pellets, although *P. antarctica* showed a near-significant relationship with these pellets at ≤10 m ($0.05 < p < 0.10$). The greatest flux of cylindrical pellets was observed at 40 m, and resembled the abundance of *O. curvata* and *P. antarctica* between 10 and 20 m, indicating these pellets persisted throughout the water column and contributed to vertical flux.

A negative relationship ($0.05 < p < 0.10$) between the abundance of *Oithona similis* and the flux of cylindrical pellets at all depths ≥5 m was observed, supporting the findings of González & Smetacek (1994) that this copepod engages in coprophagy. Coprophagy in the water column can reportedly decrease the abundance of some pellets by up to 75% (González & Smetacek 1994) and while *Oncaea curvata* dominated the copepod abundance, cylindrical pellets were the least abundant pellet-type collected in sediment traps. Cylindrical copepod pellets can contain undigested chl *a* (Bathmann & Liebezeit 1986, Nelson 1989), and it has been suggested they may provide a nutrient source for other plankton (Smetacek 1980, González et al. 1994a). However, similar to Bathmann et al. (1987), we found that cylindrical pellets were easily damaged in the laboratory and degraded during preparation for SEM. Therefore, microbial and physical degradation could also have contributed to the overall low abundance of cylindrical pellets collected in sediment traps, particularly when heterotrophy predominated in the latter half of the season (Beaumont unpubl. data). The significant positive correlation between the abundance of *O. similis* and the flux of cylindrical pellets at ≤5 m suggests that coprophagy is facultative: high concentrations of protists, such as the ice-algal mat, may provide ample food and reduce coprophagous feeding.

Cylindrical pellets could be easily identified by their overall morphology using LM. The size (>200 µm), shape (cylindrical) and optical density (opaque) were characteristic of 'typical' copepod pellets (Marshall & Orr 1955, Honjo & Roman 1978, Martens 1978). Furthermore, investigation of pellet ultrastructure using SEM showed that pellets predominantly contained compacted fragments of diatoms and occasional whole frustules reflecting raptorial feeding (González et al. 1994a), and showed little distortion of the bounding membrane.

Oval pellets

Oithona similis was abundant throughout the season and reportedly produces small oval pellets that can vary in size, even in the presence of a constant food source, ranging from 20 to 120 µm (Martens 1978, González 1994a). The abundance of *O. similis* did not significantly correlate with that of oval pellets. However, correlations ($0.05 < p < 0.10$) were observed at

≤20 m in the water column where *O. similis* was most abundant suggesting that these copepods produced oval pellets (Table 3). To our knowledge, the shape of harpacticoid pellets has not been described. However, similar to *O. similis*, harpacticoids may produce oval pellets, as a weak correlation ($0.05 < p < 0.10$) was observed between the abundance of harpacticoids and oval pellet flux.

Oithona similis, harpacticoids and oval pellets were abundant in near-surface waters. While the maximum abundance of *O. similis* and harpacticoids occurred during mid to late summer, their concentrations were around 10 times less than that of *Oncaea curvata*. However, oval pellets were up to 50 times more abundant than cylindrical pellets. Similar to González (1992a), our laboratory observations suggest oval pellets were resistant to mechanical stress and microbial breakdown, and the high abundance of these pellets in surface waters relative to the concentration of their planktonic producers suggests that they may be persistent. Cadée et al. (1992) reported that oval pellets (150 to 350 µm long) had relatively high sinking rates (80 to 250 m d^{-1}). In contrast, our results, showing high pellet abundance in surface waters and low flux to depth indicated low sinking rates and eventual pellet breakdown. Many reasons have been proposed why pellet flux is retarded in the water column (Bathmann et al. 1987, Noji et al. 1991, González et al. 1994b) and we previously suggested that the low flux of oval pellets resulted from coprophagy (Beaumont et al. 2001). However, statistical analyses did not support this as there were no substantial negative relationships between the abundance of copepods and oval pellets.

Oval pellets produced by *Oithona similis* and harpacticoids, while relatively small, contained highly compacted diatom fragments as well as intact algal frustules typical of pellets produced by cyclopoid copepods (Adrian 1987). However, similar to pellet contents described from a temperate harpacticoid species (Dahms 1993), these pellets also contained non-diatomaceous and other organic material that may contribute to their reduced sinking rates (Bienfang 1980, Hansen et al. 1996, Feinberg & Dam 1998).

Pellets with intact frustules

Pellets containing intact frustules were the second most abundant type of faecal pellet. These pellets resembled descriptions of pellets produced by protozoa (Stoecker 1984, Buck et al. 1990, Buck & Newton 1995) however, the concentration of protozoa did not significantly correlate with the abundance of these pellets. The lack of correlation may be due to a number of factors. Firstly, this may have been an artefact of our sampling methods. We did not sample protozoa in the ice and they may have contributed substantially to the abundance of pellets in the water column. Furthermore, obtaining weekly 2 l samples may not have encompassed the high spatial and temporal variability of the protozoan community. Fixation with Lugol's iodine may also have led to the loss of some organisms sampled. In addition, the accurate determination of the trophic status of dinoflagellate species is problematic, and estimates of protozoan abundance exhibited high variance due to their rare occurrence in microscope counts. Second, production of pellets may be variable due to the large amount of nutrition likely to be obtained from a single feeding event. Third, the variable abundance of these pellets may be due to high rates of degradation and disintegration of some pellets (see below).

Protozoan pellets were most abundant in the upper 10 m of the water column. They were relatively large (averaging 150 µm in diameter) but contained intact diatom frustules, greatly reducing the density of siliceous material in the pellet (see below).

A large pellet volume relative to specific weight reportedly retards pellet flux (Madin 1982), and the low abundance of these pellets we observed at depth indicates that these large protozoan pellets contributed little to vertical flux. This agrees with the finding of González (1992b), but contrasts with that of Gowing et al. (2001) who reported large protozoan pellets sedimenting to depth. The morphology of ovoid pellets reported by Gowing et al. (2001) suggests they may not be of protozoan origin. However, differences in feeding mechanisms among protozoan genera could affect pellet morphology and production, and consequently the abundance and persistence of pellets in the water column.

Our observations of the morphology and ultrastructure of pellets containing intact frustules using LM and SEM showed 3 distinct morphological types. Oval pellets appeared the most compact and robust of the pellet types, and were frequently the most abundant protozoan pellet observed in sediment traps. These pellets were membrane-bound containing mixed diatoms or single diatom species and such pellets have previously been attributed to protozoans (Nöthig & von Bodungen 1989, González 1992b). These oval pellets most resembled those produced by an athecate dinoflagellate in Antarctic sea-ice and underlying waters (Buck et al. 1990). Pasternak et al. (2000) recently reported that small larvaceans also produce oval pellets and these pellets contained only whole diatom frustules (A. Pasternak pers. comm.). However, larvaceans were not abundant in our study.

Irregular pellets were similar to those previously recorded in coastal waters (Nöthig & von Bodungen

1989, González 1992b, Buck & Newton 1995, Saito et al. 1998), and are reportedly produced by heterotrophic dinoflagellates that directly engulf their prey (Elbrachter 1991, González 1992b, Buck & Newton 1995). *Gyrodinium* spp. have been observed ingesting diatom chains and reportedly produce pellets containing monospecific diatom frustules similar to the irregular pellets we observed (Nöthig & von Bodungen 1989, González 1992, Buck & Newton 1995). Therefore, the *Gyrodinium* spp. that were abundant in our study are likely to have produced most of these irregular pellets (Table 3). However, other dinoflagellates that engulf their prey, such as heterotrophic *Gymnodinium* spp., could also have contributed to their production.

To our knowledge, the large, round, semi-transparent pellets we observed have only been reported in a single study in coastal waters off California, USA (Urrere & Knauer 1981). Their large size and contents suggest they may be the pallium of extracellular feeding dinoflagellates that engulf and digest their prey within a feeding veil (termed a pallium), enabling them to feed upon prey items larger than their own body size (Gaines & Taylor 1984, Jacobson & Anderson 1986, Schnepf & Elbrachter 1992). The pallium reportedly retracts after feeding and presumably the remains are dispersed (Elbrachter 1991). Therefore, we suggest these pellets may result from dislodgement of the pallium due to interruption while feeding, or if the pallium is renewed by the organism, and the occurrence of these pellets is likely to be rare. Members of the genus *Protoperidinium* spp. are known to be pallium-feeders (Gaines & Taylor 1984, Hansen & Calado 1999), and the *Protoperidinium* spp. we observed may have produced these pellets. Furthermore, we observed an unidentified HDIN with an apparent pallium that contained empty, compacted diatom frustules.

Minipellets

Minipellets were most abundant in the latter half of the season when HDIN and ciliates reached maximum concentration. These pellets are reportedly produced by a range of protozoa such as HDIN, ciliates, radiolarians and heterotrophic flagellates (Stoecker 1984, Gowing & Silver 1985, Elbrachter 1991, Silver & Gowing 1991). Radiolarians were not recorded in this study, and the methods we used would not have detected faeces produced by heterotrophic flagellates (see above). The abundance of HDIN, at depth intervals between 0 and 20 m, significantly correlated with the flux of minipellets to 10 and 20 m, while the abundance of ciliates at ≤10 m significantly correlated with minipellet flux to 10 m. However, neither the abundance of HDIN nor ciliates significantly correlated with the highest abundance of minipellets recorded at 40 m.

Minipellets, due to their size and morphology, are presumed to have low sinking rates and would not be expected to sink to depth (Stoecker 1984, Gowing & Silver 1985, Elbrachter 1991). However, similar to our findings, they have often been recorded in high abundance in deep waters (Gowing & Silver 1985, Nöthig & von Bodungen 1989, González et al. 1994b). The morphology of minipellets was difficult to discern using LM as they were small and generally opaque. Observations of their morphology using SEM showed there were 4 types of minipellets.

Oval minipellets, containing detritus and small diatom fragments, were observed both with and without a bounding membrane and resembled pellets produced by both dinoflagellates and ciliates (Stoecker 1984, Buck et al. 1990, Elbrachter 1991).

Small, spherical minipellets were similar in structure and contents to the dense oval pellets produced by *Oithona similis* and harpacticoids (see 'Oval pellets'), and the size of these minipellets was similar to those produced by copepod nauplii in the laboratory (Pasternak et al. 2000). Copepod nauplii were only occasionally observed in net haul samples but the mesh size of our net (100 µm) probably under-sampled these organisms (see Pasternak et al. 2000). Thus, these spherical minipellets were probably produced by copepod nauplii.

Semi-transparent minipellets containing whole diatom frustules resembled the irregular pellets that we attributed to phagotrophic dinoflagellates (see above). These pellets have previously been recorded from Antarctic waters across a broad size range (5 to 120 µm) (González 1992b), their size reportedly being determined by the quantity and species composition of available food (Elbrachter 1991). Therefore, dinoflagellates appear capable of producing faecal pellets of variable size, from minipellets to pellets comparable in size, or larger than, those produced by small copepods.

The fourth type of minipellet we observed resembled the degraded end of a cylindrical pellet and we termed these 'false minipellets'. Faecal pellets reportedly degrade as they sink (Honjo & Roman 1978, Martens & Krause 1990), and coprophagy and ablation in the water column fragments pellets and aids their degradation by microbes (Honjo & Roman 1978, Lampitt et al. 1990, Noji et al. 1991). Statistical analyses showed significant correlations between the abundances of *Oithona similis* and harpacticoids and minipellet flux to 20 and 40 m respectively. Therefore, coprophagy of cylindrical pellets by *O. similis* and harpacticoids may have contributed to the production of false minipellets. Furthermore, the lack of correlation between protozoan abundance and minipellet flux to depth suggests that false minipellets comprised the majority of mini-

pellets in sediment traps at 40 m. Therefore, production of false minipellets due to coprophagy and degradation may assist in explaining the abundance of minipellets in deep waters reported in previous studies (see above).

Most studies investigating particle flux have used only LM to examine faecal pellet morphology and abundance. While LM is necessary for quantitative analysis of sediment trap material, it limits the ability to resolve detailed structure and morphology of pellets. Under the light microscope, we observed copepod pellets that appeared free of external matter. However, when viewed using SEM, whole diatoms were observed adhered to the outer surface of the pellet that may be confused with pellet contents under the light microscope. Furthermore, previous studies have reported difficulties in distinguishing faecal pellets from protozoa when viewed by LM (Nöthig & von Bodungen 1989, Gowing et al. 2001). Therefore, we propose that the classification of faecal pellets using LM be validated using SEM.

Contribution by copepods and protozoa to vertical flux

It is generally believed that heterotrophic grazing facilitates the export of primary production, and biogenic particles greater than 100 µm are primarily responsible for vertical carbon flux in the oceans (e.g. Fowler & Knauer 1986, Williams et al. 1989, Fortier et al. 1994). However, in northern hemisphere waters, the retention of a variety of pellet types (large cylindrical, oval, protozoan, minipellets) has been observed (Smetacek 1980, Hofmann et al. 1981, Martens & Krause 1990, Wassmann et al. 1994, Vittasalo et al. 1999, Pasternak et al. 2000). In Antarctic waters there has been little consensus on the fate of faecal pellets. Large cylindrical pellets have been reported to be retained in upper waters, but in conjunction with oval pellets they can also contribute to vertical flux (Bathmann et al. 1991, Cadée et al. 1992, González 1992a, Suzuki et al. 2001). Furthermore, it has been proposed that protozoan pellets can contribute significantly to carbon export (Nöthig & von Bodungen 1989, Buck et al. 1990, Bathmann et al. 1991, González 1992a, Gowing et al. 2001). We found that small cylindrical pellets from *Oncaea curvata* and *Paralabidocera antarctica* can also sediment to depth. However, oval pellets produced by *Oithona similis* and small harpacticoid copepods, and protozoan pellets were retained in upper waters irrespective of their diverse range in size, shape and ultrastructure. Our results indicate that the contribution by microzooplankton to vertical carbon flux is largely determined by the species-specific origin of the pellets that defines their structure and morphology, rather than pellet size. Consequently, changes in community structure over fine spatial and temporal scales and due to long-term global climate change will influence the role of the plankton community in vertical carbon flux, with ramifications for the accumulation of greenhouse gases in the atmosphere.

Acknowledgements. We acknowledge the assistance of Anthony Plummer and the 1997/98 Davis station personnel, and we thank David Ritz, Graham Hosie, Kerrie Swadling, Stephen Nicol and 4 anonymous referees for their comments and discussion that greatly improved this manuscript. This research was supported by the Antarctic Science Advisory Committee Grants 963 and 2227, and an Australian Postgraduate Award.

LITERATURE CITED

Adrian R (1987) Viability of phytoplankton in fecal pellets of two cyclopoid copepods. Arch Hydrobiol 110:321–330

Atkinson A, Sinclair JD (2000) Zonal distribution and seasonal vertical migration of copepod assemblages in the Scotia Sea. Polar Biol 23:46–58

Azam F (1998) Microbial control of oceanic carbon flux: the plot thickens. Science 280:694–696

Banse K (1995) Zooplankton: pivotal role in the control of ocean production. ICES J Mar Sci 52:265–277

Bathmann UV (1996) Abiotic and biotic forcing on vertical particle flux in the Southern Ocean. In: Ittekot PSV, Honjo S, Depetris PJ (eds) Particle flux in the ocean. John Wiley & Sons, Chichester, p 243–250

Bathmann UV, Liebezeit G (1986) Chlorophyll in copepod faecal pellets: changes in pellet numbers and pigment content during a declining Baltic spring bloom. PSZN I: Mar Ecol 7:59–73

Bathmann UV, Noji TT, Voss M, Peinert R (1987) Copepod fecal pellets: abundance, sedimentation and content at a permanent station in the Norwegian Sea in May/June 1986. Mar Ecol Prog Ser 38:45–51

Bathmann UV, Fischer G, Müller PJ, Gerdes D (1991) Short-term variations in particulate matter sedimentation off Kapp Norvegia, Weddell Sea, Antarctica: relation to water mass advection, ice cover, plankton biomass and feeding activity. Polar Biol 11:185–195

Battarbee RW (1986) Diatom analysis. In: Berglund BE (ed) Handbook of holocene palaeoecology and palaeohydrology. John Wiley & Sons, Chichester, p 527–570

Beaumont KL, Plummer AJ, Hosie GW, Ritz DA (2001) Production and fate of faecal pellets during summer in an East Antarctic fjord. Hydrobiologia 453/454:55–65

Bienfang PK (1980) Herbivore diet affects fecal pellet settling. Can J Fish Aquat Sci 37:1352–1357

Bloesch J, Burns NM (1980) A critical review of sedimentation trap technique. Schweiz Z Hydrol 42:15–55

Buck KR, Newton J (1995) Fecal pellet flux in Dabob Bay during a diatom bloom: contribution of microzooplankton. Limnol Oceanogr 40:306–315

Buck KR, Bolt PA, Garrison DL (1990) Phagotrophy and fecal pellet production by an athecate dinoflagellate in Antarctic sea ice. Mar Ecol Prog Ser 60:75–84

Cadée GC, González H, Schnack-Schiel SB (1992) Krill diet affects faecal string settling. Polar Biol 12:75–80

Christian JR, Karl DM (1995) Measuring bacterial ectoen-

zyme activities in marine waters using mercuric chloride as a preservative and a control. Mar Ecol Prog Ser 123: 217–224
Dahms H (1993) Internal anatomy of female *Paramphiascella fulvofasciata* (Copepoda, Harpacticoida). Can J Zool 71: 1242–1250
Elbrachter M (1991) Faeces production by dinoflagellates and other small flagellates. Mar Microb Food Webs 5:189–204
Falkowski PG, Barber RT, Smetacek V (1998) Biogeochemical controls and feedbacks on ocean primary production. Science 281:200–206
Feinberg LR, Dam HG (1998) Effects of diet on dimensions, density and sinking rates of fecal pellets of the copepod *Acartia tonsa*. Mar Ecol Prog Ser 175:87–96
Fenchel T (1988) Marine plankton food chains. Annu Rev Ecol Syst 19:19–38
Fortier L, Le Fevre J, Legendre L (1994) Export of biogenic carbn to fish and to the deep ocean: the role of large planktonic microphages. J Plankton Res 16:809–839
Fowler SW, Knauer GA (1986) Role of large particles in the transport of elements and organic compounds through the oceanic water column. Prog Oceanogr 16:147–194
Fransz HG, González SR (1995) The production of *Oithona similis* (Copepoda: Cylopoida) in the Southern Ocean. ICES J Mar Sci 52:549–555
Froneman PW, Perissinotto R (1996) Microzooplankton grazing and protozooplankton community structure in the South Atlantic and in the Atlantic sector of the Southern Ocean. Deep-Sea Res Part A 43:703–721
Gaines G, Taylor FJR (1984) Extracellular digestion in marine dinoflagellates. J Plankton Res 6:1057–1061
Garrison DL (1991) An overview of the abundance and role of protozooplankton in Antarctic waters. J Mar Syst 2: 317–331
Gibson JAE (1998) Carbon flow through inshore marine environments of the Vestfold Hills, East Antarctica. ANARE Scientific Rep 139:1–221
Gibson JAE (1999) The role of ice in determining mixing intensity in Ellis Fjord, Vestfold Hills, East Antarctica. Antarct Sci 11:419–426
González HE (1992a) The distribution and abundance of krill faecal material and oval pellets in the Scotia and Weddell Seas (Antarctica) and their role in particle flux. Polar Biol 12:81–91
González HE (1992b) Distribution and abundance of minipellets around the Antarctic peninsula. Implications for protistan feeding behaviour. Mar Ecol Prog Ser 90:223–236
González HE, Smetacek V (1994) The possible role of the cyclopoid copepod *Oithona* in retarding vertical flux of zooplankton faecal material. Mar Ecol Prog Ser 113: 233–246
González HE, Kurbjeweit F, Bathmann UV (1994a) Occurrence of cyclopoid copepods and faecal material in the Halley Bay region, Antarctica, during January-February 1991. Polar Biol 14:331–342
González HE, González SR, Brummer GJA (1994b) Short-term sedimentation pattern of zooplankton, faeces and microplankton at a permanent station in the Bjornafjorden (Norway) during April-May 1992. Mar Ecol Prog Ser 105: 31–45
González HE, Ortiz VC, Sobarzo M (2000) The role of faecal material in the particulate organic carbon flux in the northern Humboldt Current, Chile (23° S), before and during the 1997-1998 El Niño. J Plankton Res 22:499–529
Gowing MM, Silver MW (1985) Minipellets: a new and abundant size class of marine fecal pellets. J Mar Res 43: 395–418
Gowing MM, Garrison DL, Kunze HB, Winchell CJ (2001) Bio logical components of Ross Sea short-term particle fluxes in the austral summer of 1995-1996. Deep-Sea Res Part A 48:2645–2671
Hansen B, Fotel FL, Jensen NJ, Madsen SD (1996) Bacteria associated with a marine planktonic copepod in culture. II. Degradation of fecal pellets produced on a diatom, a nanoflagellate or a dinoflagellate diet. J Plankton Res 18: 275–288
Hansen PJ, Calado AJ (1999) Phagotrophic mechanisms and prey selection in free-living dinoflagellates. J Eukaryot Microbiol 46:382–389
Harbison GR, Gilmer RW (1986) Effects of animal behaviour on sediment trap collections: implications for the calculation of aragonite fluxes. Deep-Sea Res Part A 33: 1017–1024
Hofmann EE, Klinck JM, Paffenhofer G-A (1981) Concentrations and vertical fluxes of zooplankton fecal pellets on a continental shelf. Mar Biol 61:327–335
Honjo S, Roman MR (1978) Marine copepod fecal pellets: production, preservation and sedimentation. J Mar Res 36: 45–57
Jacobson DM, Anderson DM (1986) Thecate heterotrophic dinoflagellates: feeding behaviour and mechanisms. J Phycol 22:249–258
Kirkwood JM (1993) Zooplankton community dynamics and diel vertical migration in Ellis Fjord, Vestfold Hills, Antarctica. PhD thesis, Monash University, Melbourne
Kirkwood JM, Burton HR (1987) Three new zooplankton nets designed for under-ice sampling; with preliminary results of collections made from Ellis fjord, Antarctica during 1985. Proc NIPR Symp. Polar Biol 1:112–122
Knauer GA, Karl DM, Martin JH, Hunter CN (1984) *In situ* effects of selected preservatives on total carbon, nitrogen and metals collected in sediment traps. J Mar Res 42: 445–462
Lampitt RS, Noji T, von Bodungen B (1990) What happens to zooplankton faecal pellets? Implications for material flux. Mar Biol 104:15–23
Lee C, Hedges JI, Wakeham SG, Zhu N (1992) Effectiveness of various treatments in retarding microbial activity in sediment trap material and their effects on the collection of swimmers. Limnol Oceanogr 37:117–130
Le Fevre J, Legendre L, Rivkin RB (1998) Fluxes of biogenic carbon in the Southern Ocean: roles of large microphagous zooplankton. J Mar Syst 17:325–345
Lessard EJ (1991) The trophic role of heterotrophic dinoflagellates in diverse marine environments. Mar Microb Food Webs 5:49–58
Madin LP (1982) Production, composition and sedimentation of salp fecal pellets in oceanic waters. Mar Biol 67:39–45
Marchant HJ, Thomas DP (1983) Polylysine as an adhesive for the attachment of nanoplankton to substrates for electron microscopy. J Microsc 131:127–129
Marshall SM, Orr AP (1955) The Biology of a marine copepod *Calanus finmarchicus* (Gunnerus). Oliver & Boyd, London
Martens P (1978) Faecal pellets. Fiches d'identification du zooplancton 162, ICES, Copenhagen
Martens P, Krause M (1990) The fate of faecal pellets in the North Sea. Helgol Meeresunters 44:9–19
McMinn A (1994) Preliminary investigation of a method for determining past winter tempereatures at Ellis Fjord, eastern Antarctica, from fast ice assemblages. Mem Natl Inst Polar Res Spec Issue 50:34–40
Metz C (1998) Feeding of *Oncaea curvata* (Poecilostomatoida, Copepoda). Mar Ecol Prog Ser 169:229–235
MZC2 (Marine Zooplankton Colloqium 2) (2001) Future

marine zooplankton research—a perspective. Mar Ecol Prog Ser 222:297–308
Nelson JR (1989) Phytoplankton pigments in macrozooplankton feces: variability in carotenoid alterations. Mar Ecol Prog Ser 52:129–144
Noji T (1991) The influence of macrozooplankton on vertical particulate flux. Sarsia 76:1–9
Noji TT, Estep KW, MacIntyre F, Norrbin F (1991) Image analysis of faecal material grazed upon by three species of copepods: evidence for coprorhexy, coprophagy and coprochaly. J Mar Biol Assoc UK 71:465–480
Nöthig EM, Bodungen BV (1989) Occurrence and vertical flux of faecal pellets of probably protozoan origin in the southeastern Weddell Sea (Antarctica). Mar Ecol Prog Ser 56:281–289
Pasternak A, Arashkevich E, Wexels Riser CW, Ratkova T, Wassmann P (2000) Seasonal variation in zooplankton and suspended faecal pellets in the subarctic Norwegian Balsfjorden, in 1996. Sarsia 85:439–452
Reeve MR, Walter MA (1978) Nutritional ecology of ctenophores – a review of recent research. Adv Mar Biol 15: 249–287
Rivkin RB, Legendre L (2001) Biogenic carbon cycling in the upper ocean: effects of microbial respiration. Science 291:2398–2400
Rosa F, Bloesch J, Rathke DE (1994) Sampling the settling and suspended particulate matter (SPM). In: Murdoch A, MacKnight SD (eds) Handbook of techniques for aquatic sediments sampling. Lewis Publishers, Boca Raton, p 97–129
Saito R, Kudoh S, Sato T, Watanabe K, Fukuchi M (1998) Composition of sinking particulates collected under fast ice near Syowa station, East Antarctica, in early spring and early summer, 1994. Antarct Rec 42:252–268
Schnepf E, Elbrachter M (1992) Nutritional strategies in dinoflagellates: a review with emphasis on cell biological aspects. Eur J Protistol 28:3–24
Silver MW, Gowing MM (1991) The 'particle' flux: origins and biological components. Prog Oceanogr 26:75–113
Smetacek VS (1980) Zooplankton standing stock, copepod faecal pellets and particulate detritus in Kiel Bight. Estuar Coast Mar Sci 11:477–490
Steedman HFE (1976) Zooplankton fixation and preservation. UNESCO, Paris
Stoecker DK (1984) Particle production by planktonic ciliates. Limnol Oceanogr 29:930–940
Suzuki H, Sasaki H, Fukuchi M (2001) Short-term variability in the flux of rapidly sinking particles in the Antarctic marginal ice zone. Polar Biol 24:697–705
Swadling K, Gibson JAE, Ritz DA, Nichols PD, Hughes DE (1997) Grazing of phytoplankton by copepods in eastern Antarctic coastal waters. Mar Biol 128:39–48
Tanimura A, Minoda T, Fukuchi M, Hoshiai T, Ohtsuka H (1984) Swarm of *Paralabidocera antarctica* (Calanoida, Copepoda) under sea ice near Syowa Station, Antarctica. Antarct Rec 82:12–19
Tomas CRE (1996) Identifying marine diatoms and dinoflagellates. Academic Press, California
Trull TW, Gibson JAE, Beaumont KL, Bowman J and 10 others (2001) Site holds promise for ecosystem and biogeochemical investigations. EOS Trans Am Geophys Union 82:306,311
Turner JT (1984) Zooplankton feeding ecology: contents of fecal pellets of the copepods *Temora turbinata* and *T. stylifera* from continental shelf and slope waters near the mouth of the Mississippi River. Mar Biol 82:73–83
Turner JT (2000) Feeding ecology of marine copepods: an overview of recent studies and emerging issues. Natl Taiwan Museum Spec Publ Ser 10:37–57
Urrere MA, Knauer GA (1981) Zooplankton fecal pellet fluxes and vertical transport of particulate organic material in the pelagic environment. J Plankton Res 3:369–387
Verity P, Smetacek V (1996) Organism life cycles, predation, and the structure of marine pelagic ecosystems. Mar Ecol Prog Ser 130:277–293
Verity PG, Vernet M (1992) Microzooplankton grazing, pigments, and composition of plankton communities during late spring in two Norwegian fjords. Sarsia 77:263–274
Viitasalo M, Rosenberg M, Heiskanen AS, Kosi M (1999) Sedimentation of copepod fecal material in the coastal northern Baltic Sea: Where did all the pellets go? Limnol Oceanogr 44:1388–1399
Wassmann P (1998) Retention versus export food chains: processes controlling sinking loss from marine pelagic systems. Hydrobiologia 363:29–57
Wassmann P, Martinez R, Vernet M (1994) Respiration and biochemical composition of sedimenting organic matter during summer in the Barents Sea. Cont Shelf Res 14: 79–90
Williams PJleB, von Bodungen B, Bathmann U, Berger WH and 8 others (1989) Group report: export productivity from the photic zone. In: Berger WH, Smetacek VS, Wefer G (eds) Productivity of the ocean: present and past. John Wiley & Sons, Chichester, p 99–115

Editorial responsibility: Otto Kinne (Editor), Oldendorf/Luhe, Germany

Submitted: May 6, 2002; Accepted: July 26, 2002
Proofs received from author(s): December 6, 2002

Eos, Transactions, American Geophysical Union, Vol. 82, No. 28, July 10, 2001, Pages 306, 311

Site Holds Promise for Ecosystem and Biogeochemical Investigations

Ellis Fjord, located in the Vestfold Hills of East Antarctica (68.5°S, 78°E), exhibits a range of environments, from essentially marine at its seaward end, to permanently stratified basins with hypersaline brines at its inland end. The drainage basin of the fjord contains small areas of mosses and lichens, but no higher plants, and supplies fresh water to the fjord in ephemeral summer melt streams. Direct anthropogenic inputs are negligible or non-existent, as are those from other mammals and birds. The fjord exhibits unusual biological and chemical properties, and offers the opportunity to study oceanic processes in isolation and at small scales. It also has the logistical advantage of proximity to the facilities of Australia's year-round Davis research station.

Scientific research in the fjord since the mid-1980s has resulted in a fascinating but incomplete picture. The fjord extends for over 10 km and has a very narrow and shallow (< 4 m) marine entrance, which is unusual for Antarctic fjords. A series of sills divides the fjord into basins that reach depths of over 100 m, and range in nature from largely marine near Ellis Narrows to lake-like in Small Meromictic Basin (SMB, Figure 1). SMB is cut off from the rest of the fjord by ice for 10 months of the year. Sea ice up to 2 m thick forms throughout the fjord during winter. In some summers, the ice does not break out entirely, and thick multi-year ice develops. Snow cover varies irregularly along the fjord from tens of centimeters to negligible amounts in wind-swept areas.

Mixing in the fjord occurs by two major mechanisms: tidal exchange and thermohaline convection driven by sea-ice formation in winter. The intensity of tidal mixing decreases inland along the fjord. As a result, Gravel and Middle basins are seasonally stratified, and Deep and Small Meromictic basins are quasi-permanently stratified and are anoxic below 42 m and 8 m, respectively. The flow through Ellis Narrows has recently been quantified using upward-looking acoustic Doppler current profilers.

Thermohaline convection driven by salt exclusion during the formation of sea ice strongly influences the fjord. This process has resulted in the formation of hypersaline brines that have pooled in Deep and Small Meromictic basins. In addition, on the upper slopes of Deep Meromictic Basin (DMB), there are two small sub-basins: one with a 2-m-thick layer of hypersaline water enclosed by the 20-m bathymetric contour, and the other with a 6-m-thick layer enclosed by the 32-m-contour. The existence of these shallow sub-basins of hypersaline water perched on the fjord slope within the upper mixed layer is unequivocal evidence for the active production of brine flows. These flows are analogs for processes that result in the formation of Antarctic Bottom Water. The age of the anoxic bottom water in DMB, modeled from the distribution of ^{14}C in the basin, is >5000 years. Present-day brine flows containing modern carbon do not appear to contribute significantly to the old water. However, the winter input of moderate salinity brine must be sufficient to replace small tidal losses from the surface of the anoxic water mass. Brines also form in the more seaward basins, but there they appear to be mixed into the water column by the more energetic tidal mixing in those regions.

The enclosed nature of Ellis Fjord facilitates studies of Antarctic plankton ecology in a confined body of water, obviating many of the difficulties inherent to open ocean studies. Phytoplankton succession, zooplankton development, nutrient dynamics, and the export of organic matter to depth have been studied. The sea ice diatom community is usually dominated by *Entomoneis kjellmanii* and *Nitzschia stellata* in snow-covered areas or by *Berkelaya adeliense* and *Thalassiosira australis* in bare ice areas. The succession between these two communities may be driven by increasing exposure to ultra-violet radiation, with the former community giving way to the latter as the snow cover disappears. The phytoplankton in the water column are dominated by diatoms, including many species also present in the sea ice, and flagellates including *Geminigera* sp., *Pyramimonas gelidicola*, *Phaeocystis antarctica*, and a range of autotrophic and heterotrophic dinoflagellates. Seasonal succession in the water column appears to be linked to physical forcing, with periods of stable stratification favoring diatoms and greater mixing favoring flagellates. Chlorophyll a concentrations can exceed 20 mg m^3 in summer, even under 2 m of sea ice. The overall period of primary productivity, October through May, is much longer than in other Antarctic marine environments as a result of greater water column stability.

Heterotrophic organisms, including calanoid and cyclopoid copepods, ciliates, tintinnids and amoebae are well represented in the fjord, although species diversity is limited. Only 33 zooplankton species have been identified from over 1000 samples, including some species that also have been found in Antarctic saline lakes.

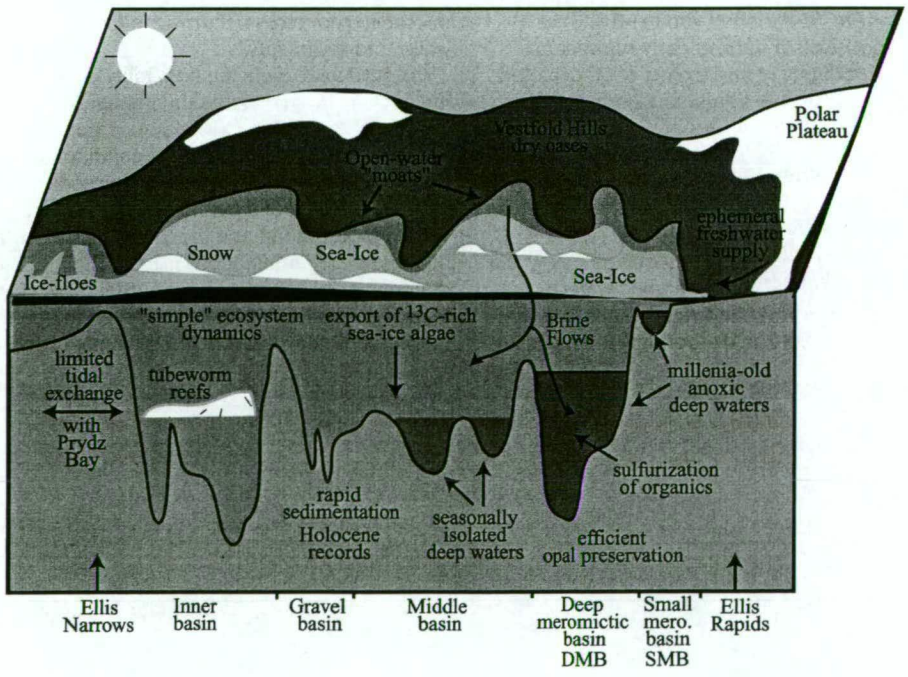


Fig. 1. Diagram of the wide range of unusual environments and processes that occur in Ellis Fjord, East Antarctica.

0096/3941/8228/306/$03.00.

The fjord environment has allowed isolated cohorts of individual species to be studied; for example, the larval development of crystal krill, *Euphausia crystallorophias*, throughout winter has been documented.

Sediment trap studies indicate that the major pulse in sedimentation occurs in summer, although a significant amount of sedimented organic carbon comes from ice algae in spring, as indicated by distinct enrichment in ^{13}C in both bulk organic carbon and diatom-specific, highly-branched alkenes. The $\delta^{13}C$ signature of organic carbon in sea ice communities during the spring bloom varies from -5‰ to -13‰, with heaviest values observed in the upper fjord over the DMB. This is significantly heavier than organic carbon collected from water column particles (-18‰ to -23‰) and surface sediments (-19.5‰) in MB. The majority of the particulate organic carbon exported from surface waters appears to be recycled within the water column, at least within the oxygenated basins. However, very small faecal pellets (5–50μ in diameter) from ciliates and other heterotrophic flagellates penetrate deeply into the water column and reach the sediments, which are rich in organic material and display only limited clastic inputs. These inputs presumably support the large colonies of the tubeworm *Serpula narcoensis* that form extensive reefs to 30-m depth in the oxic basins.

Ellis Fjord water chemistry strongly reflects both present and past biogeochemical cycling, and this is especially so for carbon. The permanently stratified DMB and SMB show an extraordinary range in the carbon isotopic composition of dissolved inorganic carbon (DIC). The surface water DIC of both basins are ^{13}C-enriched (up to +3.7‰) as a consequence of intense, early-summer primary productivity and export of ^{13}C-depleted organic carbon. A significant amount of this light carbon now resides in the hypersaline, anoxic bottom waters as a cumulative consequence of the annual cycles of productivity, export, and remineralisation, which leads to $\delta^{13}C$-DIC values as low as -16.6‰. Active methane and sulfur cycling occurs below the chemocline in DMB. The anoxic water is depleted in sulfate and rich in sulfide, with values up to 28.2 mM—perhaps the highest concentrations recorded in natural waters—and it supports communities of photosynthetic sulfur bacteria.

The environmental diversity in Ellis Fjord provides an excellent opportunity to examine the factors that control organic matter degradation and preservation in aquatic ecosystems. Organic matter is well preserved in DMB and SMB by the anoxic water column. Recent studies have highlighted the importance of sulfur incorporation into labile lipids as a preservation mechanism. This sulfur is derived from hydrogen sulfide and perhaps polysulfides. The process seems to select for certain lipid types, particularly those that contain double bonds and other functional groups. For example, sulfur incorporation into novel, highly branched isoprenoid alkenes of diatom origin has been observed, and sulfur incorporation into sterols appears to favor molecules with cholestane skeletons.

The organic geochemistry of Ellis Fjord has provided new information about the source-specificity (or lack of it) for some organic biomarker compounds. For example, the very high abundance of 24-ethylcholesterol (up to 80% of total sterols) in the sediments of DMB is surprising, as this compound is often used as a marker for higher plants that are notably absent from the area. Similarly, the sediments contain significant amounts of long-chain saturated C_{20}-C_{24} fatty acids, which are also often used as indicators of terrestrial input. Coprostanol, a sterol commonly used as a marker for human sewage, occurs at high concentrations in the sediment of the DMB, indicating that this sterol can also have non-anthropogenic sources as a result of natural microbial processes occurring in the anoxic water and sediments.

The fjord also offers the possibility of extracting records of environmental changes in coastal East Antarctica. The anoxic bottom water in DMB has created ideal conditions for the preservation of high-resolution sediment records. The lack of a benthic fauna has prevented bioturbation and the lower pH has increased the preservation of silica. The diatom record in particular is outstanding. Many lightly silicified taxa, rarely seen in open marine sediments elsewhere, are immaculately preserved. These have been used to investigate environmental change over decadal, century, and millennial time scales. For example, using changes in sea ice algal and phytoplankton communities, it is possible to identify increases in temporal sea ice cover following the end of the mid-Holocene warm period approximately 2,000 years ago.

A workshop was held recently at the Antarctic Cooperative Research Centre in Hobart, Tasmania, to develop an overview of fjord characteristics, including links between physical, biogeochemical, and ecosystem processes (as summarized in Figure 1). The workshop identified many aspects of Ellis Fjord that remain poorly understood. Examples include how much bottom water is still being formed and under what conditions, the role of the large tube worm reef colonies in removing suspended plankton, the extent to which snow and ice cover control phytoplankton production; and many other aspects of physical forcing of biological activity, such as ultra-violet exposure, extent of sub-ice meltwater accumulation, and the precise nature of sub-oxic remineralization processes. Both targeted studies and repeat investigations to address interannual variability are required. The enclosed nature of the fjord and the close proximity of different basin conditions beneath similar surface waters enhance the prospects for progress in these areas, as well as in the study of sedimentary diagenesis, ecosystem dynamics, brine flows, sea ice dynamics, and other important aspects of polar environments. More information is available from the authors, including a brief bibliography of Ellis Fjord research, from John Gibson, and via the Australian Antarctic Division Web site (www.antdiv.gov.au).

Authors

Thomas W. Trull, Antarctic CRC, University of Tasmania, Hobart, 7001, Australia; *John A. E. Gibson*, CSIRO Marine Research, GPO Box 1538, Hobart, 7001, Australia; *Karin L. Beaumont, John Bowman, Harry R. Burton, Andrew T. Davidson, Antoine Guichard, John M. Kirkwood, Andrew McMinn, Peter D. Nichols, Jenny H. Skerratt, Roger E. Summons, Kerrie M. Swadling, and John K. Volkman*

These articles have been removed for copyright or proprietary reasons.

Beaumont, KL, Plummer, AJ, Hosie, GW & Ritz, DA 2001, ‘Production and fate of faecal pellets during summer in an East Antarctic fjord’ in Lopes, RM, Reid, JW & Rocha, EF, Copepoda: Developments in Ecology, Biology and Systematics: Proceedings of the Seventh International Conference on Copepoda, held in Curitiba, Brazil, 25–31 July 1999, Developments in Hydrobiology series, vol. 156, Springer Netherlands, Netherlands.

Beaumont, KL, & Hosie, GW 1997, 'Mesoscale distribution and abundance of four pelagic copepod species in Prydz Bay' Antarctic Science, 9, pp 121-133.